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The behavioral ecology of Arctic grayling distribution in interior Alaskan streams

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THE BEHAVIORAL ECOLOGY OF ARCTIC GRAYLING DISTRIBUTION IN INTERIOR ALASKAN STREAMS

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THE BEHAVIORAL ECOLOGY OF ARCTIC GRAYLING DISTRIBUTION IN INTERIOR ALASKAN STREAMS

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ABSTRACT

During the summer months Arctic grayling in interior Alaskan streams get bigger as you travel from downstream reaches to the headwaters. On a smaller scale, within individual pools, the largest fish holds position in the middle of the current, near the deepest part of the pool, and smaller fish hold positions progressively further downstream or to the side of the pool. The results of this study support the hypothesis that a single process - competition for profitable feeding positions - produces both the whole-stream and within-pool distribution pattern.

Field experiments showed that competition for desirable positions is responsible for the distribution patterns adopted by groups of fish sharing a pool, and for the size-gradient of fish over the length of the stream. In both cases large fish excluded smaller ones from the most desirable positions. Modeling work suggested that Arctic grayling locate and rank positions on the basis of profitability. Within pools this conclusion was supported by a close fit between the positions predicted by a foraging model and the positions actually selected by Arctic grayling. Over the length of the whole stream this conclusion was supported by the model's prediction that feeding positions become more profitable as you go upstream.

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GENERAL INTRODUCTION

During the summer months, Arctic grayling in interior Alaskan streams get bigger, as you travel from downstream reaches to the headwaters (Tack 1974). On a smaller scale, within individual pools, the largest fish holds position in the middle of the current, near the deepest part of the pool, and smaller fish hold positions progressively further downstream, or to the side of the pool (Vascotto 1970; Vascotto and Morrow 1973). The goal of this study was to see if a single explanation can account for both the whole-stream and within-pool distribution patterns that I have just described. The explanation I set out to test was that fish locate and rank feeding position on the basis of profitability, and that competition for profitable positions sorts fish, until each individual occupies the most profitable position that its size allows it to defend.

This explanation for Arctic grayling distribution is based on the theory of habitat selection, by territorial animals in heterogeneous habitats, developed by Whitham (1980), from the ideas of Fretwell and Lucas (1970). In fact there are several parallels between Whitham's work on the distribution of *Pemphigus* aphids on the leaves of their primary host, and the distribution of Arctic grayling in the pools of mountain streams. In both situations spatial variation in habitat quality acts as the template for the final distribution pattern of the animals; and in both situations competition for the most profitable positions is the process that matches the distribution of the population to this template. Southwood's (1977) ideas, on habitat as a template for ecological strategies, were also important in forming my perspective on fish distribution patterns; his ideas will be even more useful

in developing an explanation for Arctic grayling migration, a problem which encompasses the questions about summer distribution patterns dealt with in this work.

This study can be viewed as two parallel investigations into the same problem. The first of these investigations deals with the question - Does competition for desirable positions sort fish into the observed distribution patterns? This question concerns the *mechanism* that produces the distribution patterns, it does not deal with the *reason* fish prefer one position over another. Field experiments were used to address this question, both for groups of fish sharing a pool (Chapter 2), and for populations of fish over the whole stream (Chapter 4). By manipulating the number, and sizes, of fish in the habitat (single pools or the whole stream) it was possible to determine whether Arctic grayling do rank positions according to desirability, and if competition does sort fish, so that the dominance rank of each individual corresponds to the rank desirability of its position.

The second investigation compliments the first by seeking to explain the basis on which fish select and rank positions. It deals with the question - Why do fish prefer one position over another? Foraging models were used to test the hypothesis that fish select and rank positions on the basis of net energy intake rate, and that they prefer the positions which allow them to maximize this rate. Behavioral ecologists regularly use models to test hypotheses about the adaptive significance of behavior, and the advantages and pitfalls of the approach are well known (Williams 1966; Krebs and Davies 1981; Stephens and Krebs 1986; Stamp-Dawkins 1986; Mangel and Clark 1988). Chapter 1 describes a foraging model that Larry Dill and I developed, to test the hypothesis that solitary Arctic grayling choose positions

which maximize their net energy intake rate. Chapter 3 describes how I developed this model, to test the hypothesis that members of dominance hierarchies select and rank positions on the basis of net energy intake rate. Finally, in Chapter 4, Jim Reynolds and I used the model to test the hypothesis that feeding positions in headwater reaches are more profitable than positions further downstream.

CHAPTER 1

Position Choice by Drift-Feeding Salmonids: a Model and a Test for Arctic Grayling *(Thymallus arcticus)* in Subarctic Mountain Streams, Interior Alaska[1]

Abstract

We develop a model to predict position choice of drift-feeding stream salmonids, assuming a fish chooses the position that maximizes its net energy intake rate. The fish's habitat is represented as a series of stream cross-profiles, each divided into vertical strips characterized by water depth and velocity. The fish may select a focal point in any of these strips, and include several neighbouring strips in its foraging area. The number of prey the fish encounters depends on its reaction distance to prey, water depth, and water velocity; the proportion of detected prey the fish is able to capture declines with water velocity. The fish's net energy intake rate is its gross energy intake rate from feeding minus the swimming cost calculated by using water velocity at the fish's focal point. There was a close match between the positions predicted by this model and those chosen by solitary Arctic grayling *(Thymallus arcticus)* in the pools of a mountain stream in Alaska.

[1] This chapter has been published as Hughes, N. F., and L. M. Dill. 1990. Canadian Journal of Fisheries and Aquatic Sciences 47: 2039-2048.

Introduction

Drift feeding fish return to the same position, or "focal point", after each excursion to catch passing prey (Newman 1956; Kalleberg 1958; Jenkins 1969; Bachman 1984). Why do fish prefer one position over the multitude of alternatives? Several authors have proposed that fish select a position where the trade-off between swimming cost and the supply of drifting food, both of which increase with water velocity, maximizes net energy gain (Newman 1956; Jenkins 1969; Bachman 1981, 1984; Fausch and White 1981; Fausch 1984). Some authors add that the proximity of overhead cover, as a refuge from predators, is also important (Newman 1956; Jenkins 1969; Fausch and White 1981; Wilzbach 1985).

Despite this general consensus only Fausch (1984) has used these ideas to develop a quantitative model to predict feeding position choice by stream dwelling salmonids. Fausch's model worked well for predicting the position chosen by the dominant coho salmon *(Oncorhynchus kisutch)* in an artificial stream tank. However, we found his model to be poor at predicting the positions chosen by Arctic grayling *(Thymallus arcticus)* in stream pools, because it over-simplifies calculation of the fish's feeding rate. Fausch assumes that fish catch all prey passing through a "window" shaped like a pie slice (1/8th of a circle with a radius of two fish lengths), and uses the fastest water velocity, within two body lengths of the fish's focal point, to estimate the number of prey passing through this window. This method takes no account of water depth, the shape of the fish's reaction field, variations in water velocity within the fish's foraging area, or the influence of water velocity on the fish's ability to capture prey.

We propose a model to predict position choice by solitary stream salmonids that differs from Fausch's (1984) model in several ways. To estimate the rate at which the fish sees prey of different sizes we use data on the size-frequency distribution of prey, the fish's reaction distance to these prey, the topography of the stream bed, and the pattern of water flow. This approach owes much to the work on reaction distances, reaction fields and volumes, and prey selectivity of lake dwelling zooplanktivores (Confer and Blades 1975; Luecke and O'Brien 1981), recently applied to prey selection by drift-feeding salmonids (Dunbrack 1984; Dunbrack and Dill 1983, 1984; Grant and Noakes 1986). The model also includes a relationship for a decline in the fish's prey capture efficiency as water velocity increases. We use this model to predict position choice by solitary Arctic grayling in the pools of a mountain stream, and compare these predictions to the positions actually selected.

Methods

We first present our model, showing how habitat data and the fish's visual abilities are used to describe a fish's foraging area, how water velocity influences prey capture efficiency, and how these combine to determine the fish's net energy intake rate. We then apply our model to predict position choice of Arctic grayling.

A. The model

Habitat and foraging area

Most pools of a mountain stream resemble one another in general morphology. A narrow, shallow jet of fast water enters the head of the pool, slows and disperses as it reaches the deeper belly of the pool, and finally enters the extensive shallow tail of the pool, where it may accelerate. We describe this architecture with a series of cross-profiles taken at 50 cm intervals along the length of the pool. We represent each cross-profile as a series of strips extending from the water surface to the stream bed. These strips are 25 cm (or occasionally 50cm) wide, characterised by water depth and velocity, and centered on the position where depth and velocity are measured (Fig. 1.1).

The fish may select a focal point in any of these strips and include several neighbouring strips in its foraging area. Its focal point is equidistant from each side of the chosen strip and (for simplicity) a quarter of the way from the stream bed to the water surface.

Maximum capture distance

Imagine a fish feeding in swift water. To capture a passing prey item it must first see the prey and then intercept it before the prey is swept downstream. The proportion of prey that it sees, and is able to capture, should decline as water velocity increases. We have modelled the form of this decline in capture efficiency using the concept of "maximum capture distance" (MCD), which is

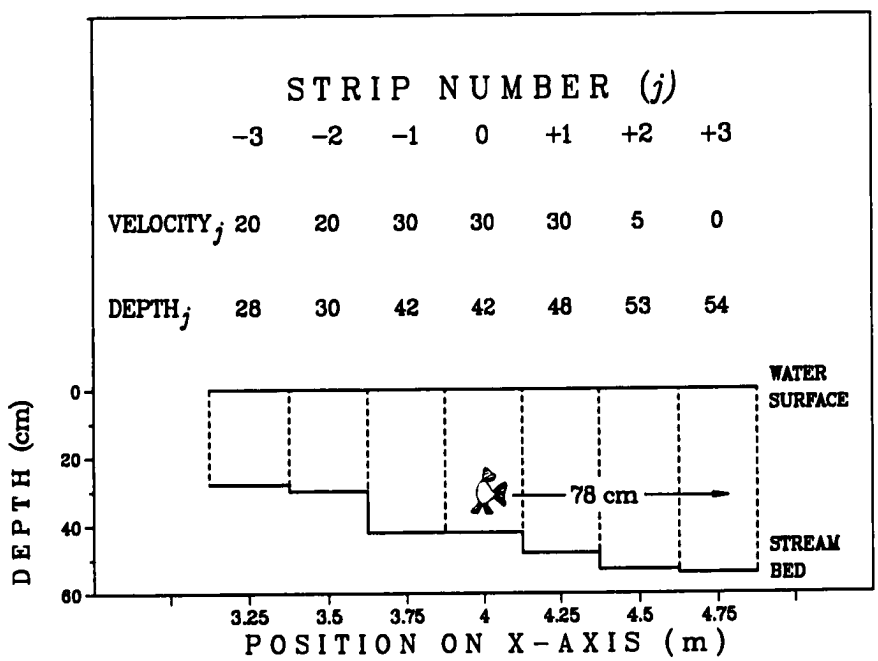


Fig. 1.1. Part of a stream cross-profile, looking upstream, showing how the habitat and the grayling's foraging space are described. Seven strips j ($j = {}^{-}3, \ldots, {}^{+}3$) are shown, each characterised by a water velocity and depth measurement. The fish's focal point is in strip 0 and, because the fish's reaction distance to the largest prey is 78 cm (see later), the seven strips encompass its foraging area.

the maximum distance from the fish's focal point, perpendicular to the current, at which the fish can intercept prey of a particular size (Note: this term was first used by Wankowski and Thorpe (1979); our definition is similar to theirs, but more restrictive.). To derive a relationship for MCD we assume that the water velocity in the fish's foraging area is V, that the fish detects each prey item at its reaction distance (RD), that the fish begins intercepting each prey item as soon as it sees it - i.e., there is no time lag, but see Godin and Rangley (1989) - and travels at its maximum sustainable swimming speed ($VMAX$). We constrain the fish to capture prey items before they cross a line perpendicular to the current passing through the focal point. This assumption is not realistic but there is little information available with which to improve it.

Under these conditions the relationship between MCD and RD, $VMAX$, and V can be derived as follows (Fig. 1.2). When line segment $AC = MCD$, the time it takes the fish to travel this distance (Time fish = TF) will be the same as the time taken by the prey to travel line segment BC (Time prey = TP), and the fish will catch the prey just as it crosses line DE. To travel AC, relative to the streambed, the fish must swim AB relative to the water. $AB = RD$ and $BC = V \cdot TP$ and since $TP = TF = RD/VMAX$, then by substitution $BC = V \cdot RD/VMAX$.

Therefore, using Pythagoras' theorem:

$$MCD = \sqrt{RD^2 - (V \cdot RD/VMAX)^2} \quad (1)$$

The relationship between maximum capture distance and water velocity is illustrated in Fig. 1.3, for several combinations of RD and $VMAX$. (Note that both

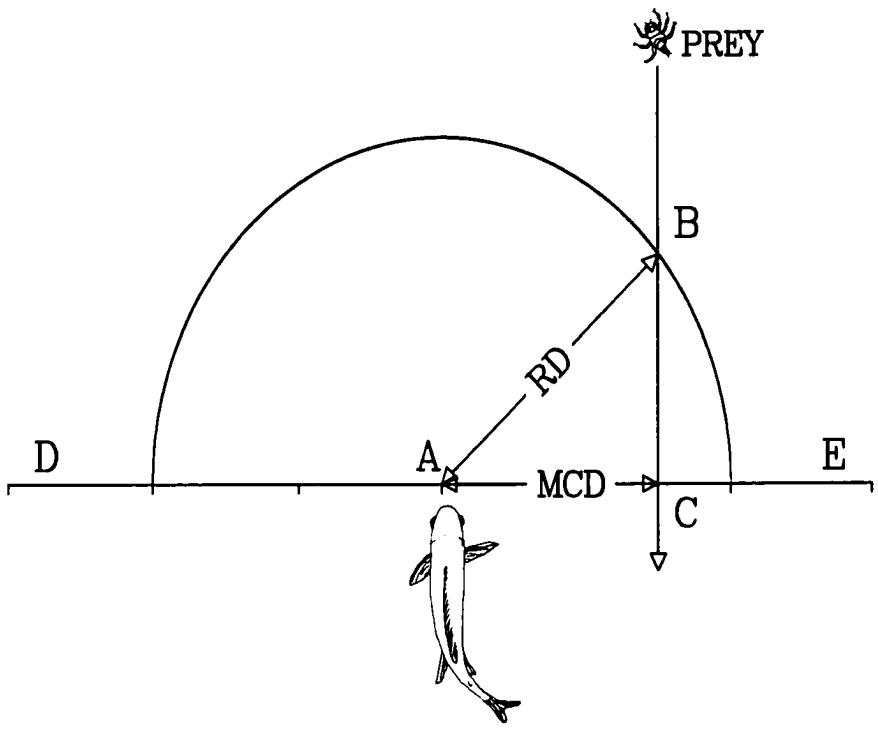


Fig. 1.2. Geometry of prey interception, seen from above. A is the fish's focal point, AB its reaction distance to the approaching prey, and AC the maximum capture distance. The fish will see the prey at B and must intercept it before it crosses the line DE.

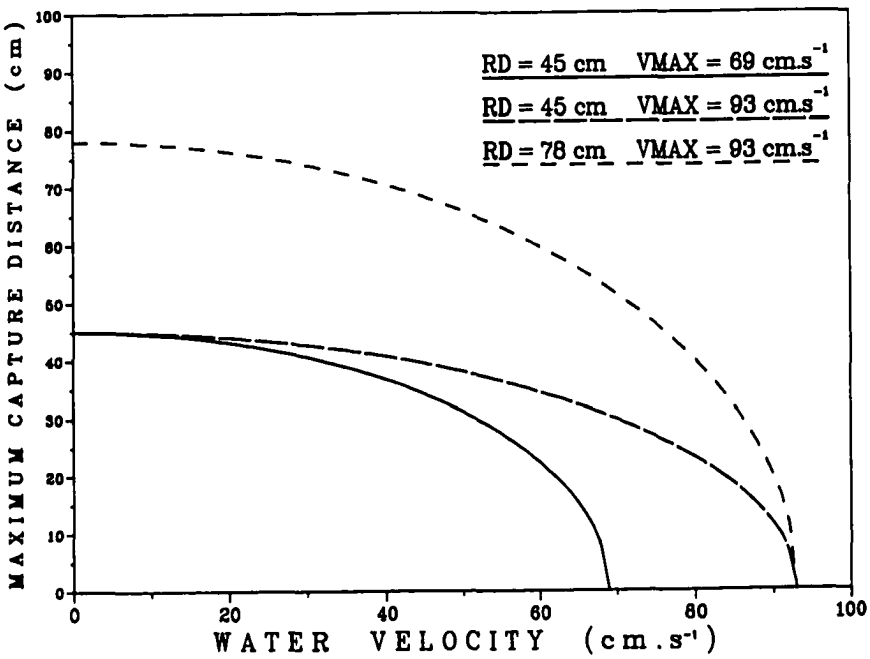


Fig. 1.3. Relationship between the maximum capture distance and water velocity, showing the influence of reaction distance (*RD*), and interception speed (*VMAX*).

RD and $VMAX$ are expected to depend on fish size.) This is a two dimensional argument but can be generalized to three dimensions, as below.

Calculating net energy intake

The fish's net energy intake rate is the balance of its gains from feeding and its swimming cost. To estimate the fish's feeding rate we first calculate the cross sectional area of each strip j ($j = {}^{-}3, \ldots, {}^{+}3$), within which the fish will capture prey in each of three size-classes i ($i = 1, 2, 3$). Figure 1.4 shows how these capture areas (CA_{ij}) are defined.

Once the values of CA_{ij} are known it is possible to calculate the total energy content of the prey passing within capture range of the fish, or gross energy intake rate (GEI), as follows:

(2)

$$GEI = \sum_{i=1}^{3} \sum_{j=-3}^{+3} CA_{ij} \cdot V_j \cdot PC_i \cdot PE_i \cdot 3,600/1,000,000$$

where V_j is the average water velocity in strip j, PC_i is the concentration of prey in size class i, and PE_i is the energy content of prey in size-class i. The $3,600/1,000,000$ term is necessary because CA_{ij} and V_j have units of centimeters and seconds while PC_i and GEI have units of meters and hours.

We use the water velocity at the fish's focal point (eg. V_0 in Fig 1.1) to calculate swimming cost (SC), i.e., we ignore the small incremental cost of prey attack. Net energy intake rate (NEI) is then simply: $NEI = GEI - SC$.

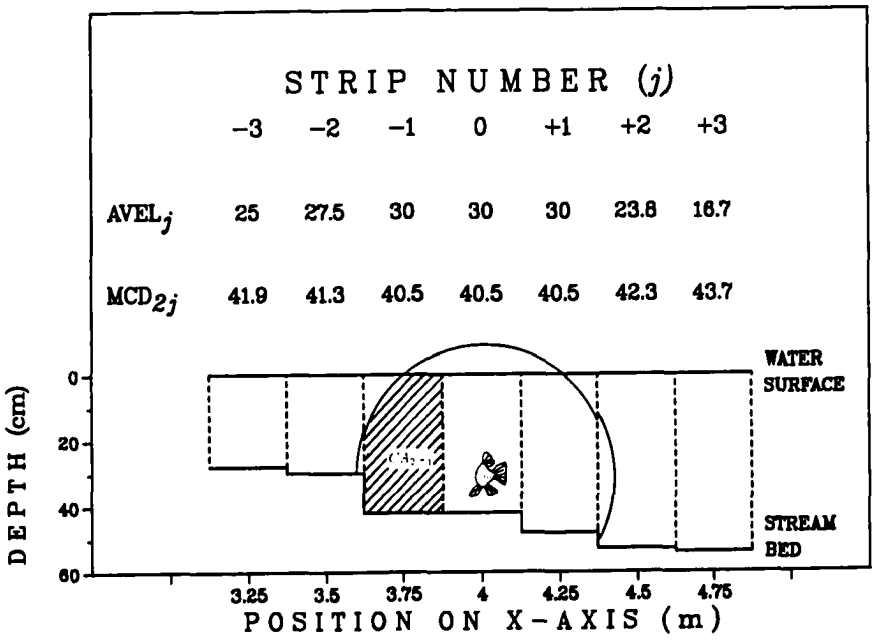


Fig. 1.4. Area within which the fish can capture prey in size-class $i = 2$. The $AVEL_j$ are the means of the water velocities in the strips the fish must cross to intercept prey in strip j, weighted by the average distance the fish travels in each strip. The MCD_{2j} are the maximum capture distances for prey in size-class $i = 2$ appropriate for strip j. These are calculated using Eqn. 1, in which $RD = 45$ cm (the appropriate RD for prey in size-class $i = 2$), $V = AVEL_j$, and $VMAX = 69$ cm·s^{-1} (the appropriate $VMAX$ for a 30 cm grayling). The areas of each strip j within which the fish will capture prey in size-class i (CA_{ij}) are the overlaps between strip j and a circle with radius MCD_{ij} centered on the fish's focal point. $CA_{2,-1}$ is shaded. Note that this is the same cross section as illustrated in Fig. 1.1 and that the radii of the arcs that encompass the CA_{2j} happen to be the same for strips -1, 0, and +1 but not for strips -2 or +2.

B. Application of the model to predict position choice of grayling

Position choice experiments

We performed position choice experiments during the summers of 1986 and 1987 in the pools of Twelvemile Creek, a second order mountain stream (at about 65° 25' N, 145° 30' W), Yukon River Drainage, Interior Alaska.

To provide an XY coordinate system with which to record the location of habitat measurements, and the position choice of grayling, we laid a grid consisting of 1 m squares on the stream bed, using 3-mm white nylon cord. The X axis of this grid was parallel to the current. We mapped Yellow Flower Pool on 7 September 1986 and 14 July 1987, Waterfall Pool on 15 September 1986, and Bedrock Pool on 3 September 1987. In Yellow Flower Pool and Bedrock Pool water depth and average water velocity were measured at 0.5 m intervals on the X-axis and 0.25 m intervals on the Y-axis, except in the tail of each pool, where measurements were 0.5 m apart on both axes. In Waterfall Pool the measurement interval was 0.5 m on both axes and we interpolated values to give a 0.25 m interval on the Y-axis. Water velocity was measured with a Marsh McBirny current meter.[1] We did not map the pools at the same time we recorded fish position, however, fish occupied the same positions at the time of mapping as in the position choice experiments we report here.

The grayling in Twelvemile Creek take advantage of the long summer days to feed continuously, often maintaining the same feeding position twenty four hours

[1] Reference to trade names or manufacturers does not imply government endorsement of commercial products.

a day (NFH, pers. obs.). Evidently they rarely become satiated, when we would expect them to move to low velocity resting positions. Occasionally fish do select resting positions, but this is apparently in response to very low drift abundance, not satiation. Their behavior makes it possible to determine a grayling's preferred feeding position quite easily, and describe it with a single XY coordinate.

To prepare for the position choice experiments we blocknetted the upstream and downstream ends of each pool to prevent wild fish from entering, and removed unwanted resident fish with rod and line or seine. Most experimental fish were caught with rod and line and introduced into the pools soon after capture, but one was a natural resident. We ran two position choice experiments in each of four pools (Yellow Flower Pool 1986 and Yellow Flower Pool 1987 are considered separately because bottom topography and pattern of water flow changed markedly during the spring break up of 1987); the design of these experiments is given in Table 1.1. We observed the fish from a camouflaged observation tower 4 m high, and recorded each fish's focal point on a scale map of the pool. To assign coordinates to each fish's position we rounded the location of its focal point to the nearest 0.5 m on the X-axis and the nearest 0.25 m on the Y-axis.

Parameters obtained from the literature

All parameters, other than data on water depth and velocity, were derived from the literature. To estimate the concentration of drifting invertebrates we used an equation developed by LaPerriere (1981, 1983) for Interior Alaskan streams in the immediate vicinity of Twelvemile Creek. This equation describes the relationship between the mean summer concentration of drifting invertebrates at a station and

Table 1.1. Design and results of position choice experiments - showing fork lengths of fish used in each pool, dates of introduction and observation, and the coordinates of the positions selected by the fish, predicted by our model, and predicted by Fausch's (1984) model.

	Date introduced	Date observed	XY Coordinates of selected position	XY Coordinates of predicted position (This paper)	XY Coordinates of predicted position (Fausch 1984)
Yellow Flower Pool 1986					
200 mm fish[a]	10 July 1986	11 July 1986	6.50, 3.50	6.50, 3.75	1.00, 2.25
280 mm fish	9 July 1986	10 July 1986	6.50, 3.50	6.00, 3.75	0.50, 3.50
Waterfall Pool 1986					
193 mm fish[a]	10 July 1986	11 July 1986	3.00, 2.00	2.50, 2.25	0.50, 2.50
325 mm fish	8 July 1986	10 July 1986	4.00, 2.00 and 3.00, 2.00	2.50, 2.25	0.50, 2.50
Yellow Flower Pool 1987					
275 mm fish[a]	19 July 1987	21 July 1987	7.50, 3.75	6.50, 4.00	0.00, 4.00
300 mm fish	6 August 1987	7 August 1987	7.50, 3.75	6.50, 4.00	0.00, 4.00
Bedrock Pool 1987					
250 mm fish[a]	4 August 1987	5 August 1987	6.50, 4.25	5.50, 4.25	1.00, 5.00
280 mm fish	Natural resident	19 July 1987	6.50, 4.50	7.00, 4.00	1.00, 5.00

[a]The positions of these fish are illustrated in Figure 5.

the mean summer discharge at that station, allowing us to predict invertebrate drift concentration in our experimental pools from stream discharge data. We used data from Imnaviat Creek (Table 1.2), a beaded tundra stream in Northern Alaska, to approximate the size composition of the drift (Ries 1988). In both Imnaviat Creek, and Interior Alaskan streams, chironomids dominate the invertebrate fauna (Oswood 1989), and the mean size of drifting invertebrates is very similar (0.59 mg in Imnaviat Creek, based on Table 1.2 and the length/weight relationship given in Rogers et al. (1976), and 0.63 mg in LaPerriere's study of Interior Alaskan streams). These similarities make us comfortable applying size composition data from Imnaviat Creek to Twelvemile Creek. Note that floating food items and possible localized inputs from cover vegetation are not accounted for by the model.

The equations we used to estimate the abundance and energy content of the prey, the reaction distance of fish to these prey, and the swimming performance of grayling are given in Table 1.3.

Values for prey abundance, prey energy content, and reaction distance, for the three prey size-classes are given in Table 1.4. Reaction distance increases asymptotically with fish length but hardly changes for fish over 19 cm in length, so we used the same values for all the fish in our experiments. Values of $VMAX$ ranged from 63 $cm \cdot s^{-1}$ for the smallest fish to 71 $cm \cdot s^{-1}$ for the largest fish. Swimming cost varied with water velocity at the focal point, and with fish size.

Predicting position choice

To predict fish position choice we use our model to estimate the fish's NEI at all possible focal points in a pool (for comparison we did the same using Fausch's

Table 1.2. Length-frequency of invertebrate drift in Imnaviat Creek, summer 1985 (Ries 1988).

i	Size-class i (mm)	PL_i Midpoint of size-class i (mm)	PP_i Proportion of prey in size-class i
1	0.5-2.5	1.50	0.58
2	2.6-5.0	3.75	0.38
3	5.1-8.0	6.50	0.04

Table 1.3. Equations used to estimate parameters in the model, and their sources. PC_i is the abundance of prey in size-class i, PE_i is the energy content of prey in size-class i, RD_i is the reaction distance of the fish to prey in size-class i, $VMAX$ is the fish's maximum sustainable swimming speed, SC is the fish's swimming cost. V is the average water velocity at the fish's position ($cm \cdot s^{-1}$), PP_i and PL_i are parameters from Table 1.2. FL is fish fork length (cm), FW is fish weight (g) which was estimated from fish length by regression ($Log(FW) = -2.03 + 3.03 \cdot Log(FL)$), SF is mean summer discharge, this was about 0.25 $m^3 \cdot s^{-1}$ in the study reach (unpubl. data).

Parameter	Units	Equation	Source
PC_i	$no.m^{-3}$	$PC_i = PP_i \cdot e^{(-0.45 \cdot Ln(SF) - 1.702)}$	Adapted from LaPerriere (1981).
PE_i	joules	$PE_i = 0.7274 \cdot PL_i^{2.62}$	Adapted from Cummins and Wuycheck (1971) and Rogers et al. (1976).
RD_i	cm	$RD_i = 12 \cdot PL_i(1 - e^{(-0.2 \cdot FL)})$	Estimated from data given by Schmidt and O'Brien (1982)[a].
$VMAX$	$cm.s^{-1}$	$VMAX = 36.23 \cdot FL^{0.19}$	Jones et al. (1974).
SC	$joules.h^{-1}$	$SC = 10^{(C + M \cdot V)} \cdot 19 \cdot FW/1000$	Derived from graphical models in Brett and Glass (1973)[b].
		where $C = 2.07 - 0.37 \cdot Log(FL)$	
		and $M = 0.0410 - 0.0196 \cdot Log(FL)$	

[a] Developed using data for 3 - 13 cm grayling feeding on Arctic zooplankton at 1354 Lux.

[b] Using data for sockeye salmon *(Oncorhynchus nerka)* at 10 °C.

Table 1.4. Values for prey concentration (PC_i), prey energy content (PE_i) and reaction distance (RD_i) for each size-class of prey, calculated by using equations from Table 1.3.

Size-class (mm)	PC_i Prey density ($no.m^{-3}$)	PE_i Prey energy content (joules)	RD_i Reaction distance (cm)
0.5-2.5	0.1976	2.10	18
2.6-5.0	0.1295	23.21	45
5.1-8.0	0.0136	98.08	78

(1984) model). The number of possible focal points equals the number of strips in all the cross-sections taken to describe the pool. The XY coordinates of these possible focal points correspond to the XY coordinates at which water depth and water velocity were measured. We predict the grayling will choose the focal point where NEI is greatest. These calculations also allow the construction of a NEI contour map for the pool.

Results

The positions predicted by our model are quite close to those selected by the grayling (Table 1.1) and similar in physical character, lying in the center of the current near the deepest part of the pool (Fig. 1.5, Table 1.5). By comparison the positions predicted by Fausch's (1984) model are much further from the positions selected by the grayling, and quite different in physical character, lying in slow water at the head of the pool, within two fish lengths of very fast water.

In each of the pools both fish selected the same (3 pools), or very similar (1 pool) positions. The larger fish in Waterfall Pool did use a second position that was distinctive from the one used by the smaller fish, but this appeared to be a resting position rather than a feeding position. Each of the models also predicted the same, or similar positions, for both the fish in each pool (Table 1.1).

On average our model ranked the positions selected by the fish in the top 4% of available positions while ranks for the positions predicted by Fausch's (1984) model were much lower (Table 1.5).

To show how our model functions, we compared the predictions of the full model to two reduced versions (Table 1.6). In reduced version A the fish pays no

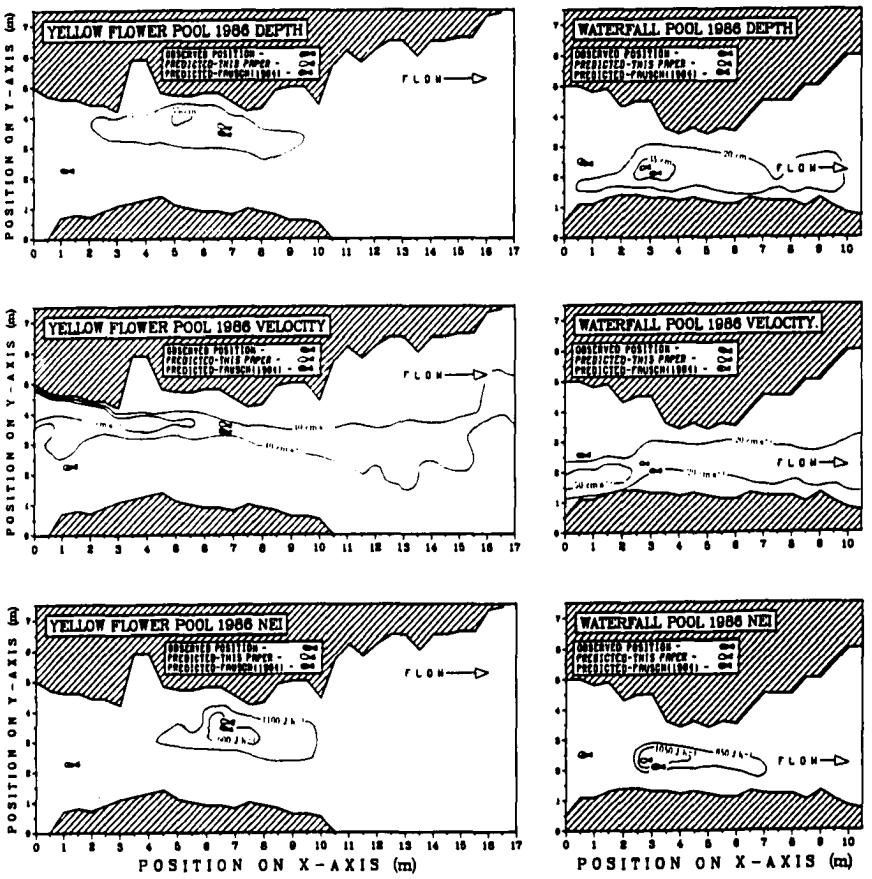


Fig. 1.5. Observed and predicted fish position choices, in relation to water depth (cm), water velocity (cm·s^{-1}), and predicted net energy intake (*NEI*; J·h^{-1}), for 200 mm fish in Yellow Flower Pool (1986), 193 mm fish in Waterfall Pool (1986), 275 mm fish in Yellow Flower Pool (1987), and 250 mm fish in Bedrock Pool (1987).

Fig. 1.5 cont.

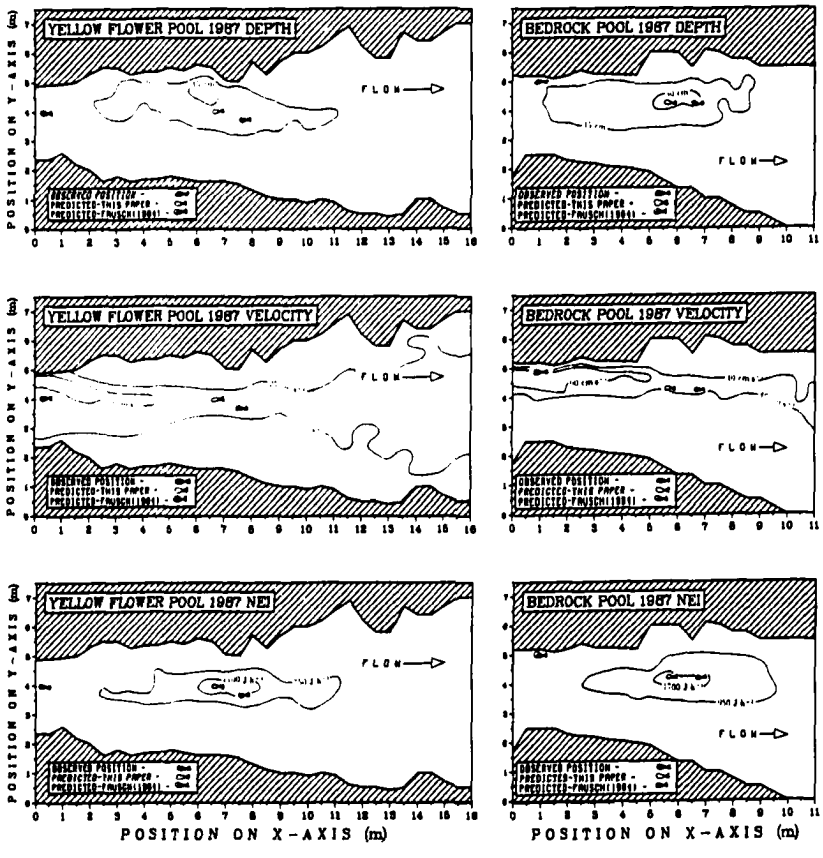


Table 1.5. Comparison of physical features at positions selected by the fish with the positions predicted by our model and by Fausch's (1984) model, showing water depth and velocity at each position, and the fastest velocity within two fish lengths either side of each position. Also shown are the ranks our model gave to each position. Only one fish from each of the four pools is included in this table, because positions selected by the second fish were identical or very similar (see Table 1.1).

	Water depth (cm)	Water velocity ($cm \cdot s^{-1}$)	Fastest water within two fish lengths ($cm \cdot s^{-1}$)	Ranking of position by our model
Yellow Flower Pool 1986 - 200 mm fish				
Observed position	56	50	50	9^{th} out of 477
Predicted - this paper	50	40	50	1^{st} out of 477
Predicted - Fausch(1984)	10	0	100	338^{th} out of 477
Waterfall Pool 1986 - 193 mm fish				
Observed position	43	20	28	22^{nd} out of 286
Predicted - this paper	37	33	40	1^{st} out of 286
Predicted - Fausch(1984)	5	0	35	134^{th} out of 286

Continued...

Table 1.5. Continued.

	Water depth (cm)	Water velocity ($cm \cdot s^{-1}$)	Fastest water within two fish lengths ($cm \cdot s^{-1}$)	Ranking of position by our model
Yellow Flower Pool 1987 - 275 mm fish				
Observed position	42	25	30	2^{nd} out of 486
Predicted - this paper	42	30	30	1^{st} out of 486
Predicted - Fausch(1984)	17	5	110	155^{th} out of 486
Bedrock Pool 1987 - 250 mm fish				
Observed position	50	55	55	10^{th} out of 318
Predicted - this paper	54	40	45	1^{st} out of 318
Predicted - Fausch(1984)	34	10	130	229^{th} out of 318

Table 1.6. Coordinates of feeding positions predicted by the full model and two reduced models for Yellow Flower Pool (1986), Waterfall Pool (1986), Yellow Flower Pool (1987), and Bedrock Pool (1987), Twelvemile Creek.

	Predicted position		
	Full model	Reduced version A (no swimming costs)	Reduced version B ($MCD = RD$)
Yellow Flower Pool 1986			
200 mm fish	6.50, 3.75	6.00, 3.75	4.00, 3.25
280 mm fish	6.00, 3.75	6.00, 3.75	4.00, 3.25
Waterfall Pool 1986			
193 mm fish	2.50, 2.25	2.50, 2.25	2.00, 1.75
325 mm fish	2.50, 2.25	2.50, 2.25	2.50, 2.25
Yellow Flower Pool 1987			
275 mm fish	6.50, 4.00	6.50, 4.00	3.00, 3.75
300 mm fish	6.50, 4.00	6.50, 4.00	3.00, 3.75
Bedrock Pool 1987			
250 mm fish	5.50, 4.25	5.50, 4.25	2.00, 4.50
280 mm fish	7.00, 4.00	5.50, 4.25	2.00, 4.50

swimming cost, while in version B maximum capture distance is independent of water velocity, remaining at the fish's reaction distance. The predictions of version A are the same, or very close, to those of the full model, while the positions predicted by version B are mostly further upstream, in the center of fast current, at the head of the pool.

Discussion

The similarity between the positions predicted by our model and those selected by the grayling supports the hypothesis that grayling choose positions which maximize their net energy intake rate. Our model's predictions are substantially more accurate than those of the only other available model (Fausch 1984), because our model includes more realistic assumptions about the number of prey the fish detects and the influence of water velocity on the prey capture abilities of the fish.

The prevailing view - that fish maximize their net energy intake rate by selecting a water velocity that optimizes the trade-off between food supply and swimming cost (Jenkins 1969; Bachman 1981,1984; Fausch and White 1981; Fausch 1984) - is probably too simple. Removing swimming cost from our model results in little or no change in its predictions, demonstrating that trade-offs involving cost are not necessary to predict position choice in this particular situation. This is because the spatial variation of swimming costs and gross energy intake are such that the position that provides the greatest gross energy intake also provides the greatest net energy intake, after the subtraction of swimming costs. This does not mean that swimming costs are unimportant; at lower drift densities

than we use here, trade-offs involving costs become important in determining the predicted position (Hughes and Dill in prep.).

There is an important trade-off in our model between the number of prey items that a fish sees, and the proportion of these it is able to capture. The number of prey the fish sees increases with water depth and velocity, compared to only velocity in Fausch's model, while the proportion of detected prey the fish is able to capture declines with water velocity (there is no such decline in Fausch's model). The importance of this trade-off is shown by comparing the predictions of the full model with those of reduced version B, in which the fish catches all the prey it sees, irrespective of water velocity. The predictions of version B are considerably poorer than those of the full model.

Several authors have suggested that overhead cover influences choice of feeding positions by stream salmonids (Newman 1956; Jenkins 1969; Fausch and White 1981), implying that fish select positions that optimize the trade-off between net energy intake rate and predation risk. This idea is appealing because predation risk may be high in well-lit midstream positions, which allow the highest net energy intake rate, and low beneath overhead cover, where light conditions reduce the ability of fish to see prey (Wilzbach 1985). In addition, it has been shown that fish do trade off predation risk and food intake rate in many situations (Werner et al. 1983; Power 1984; Dill and Fraser 1984; see Dill 1987 for a review).

Predation risk may not be an important determinant of position choice for relatively large fish, however. In this study grayling selected positions in the deepest (Yellow Flower Pool) or second deepest (Bedrock Pool) depression, in the center of the current. These positions were often a long way from the "bolt

holes" they used to hide in when alarmed. Jenkins (1969) gave a very similar physical description for the positions chosen by brown trout *(Salmo trutta)* and rainbow trout *(Oncorhynchus mykiss)* in a semi-natural stream channel, and found that fish chose the same positions soon after channel construction that they chose later, when overhead cover had developed. Similarly, Bachman (1984) showed that brown trout in his study pool spent most of their time feeding in midstream, clearly visible from overhead. These observations suggest that large salmonids select their feeding positions on the basis of water depth and flow, not on the proximity of overhead cover.

Applications of the model and future developments

By varying the values of parameters in our model it should be possible to explain a wide range of position choice behavior. For example - some parameters, such as $VMAX$, swimming cost, and reaction distance depend on fish size, while others such as prey size and prey concentration depend on location, time of day, and season. Preliminary simulation results suggest that these variations can explain why stream salmonids move into faster deeper water as they grow, and change their positions daily and seasonally (Hughes and Dill in prep.). Ideas incorporated in this model have already been used to predict the size composition of the diet (Dunbrack and Dill 1983; Grant and Noakes 1986).

In future it should be easy to adapt our model to include more information on the environmental variables that affect a fish's energy intake. Two useful relationships might be the influence of temperature on swimming costs, which could be included using data from Brett and Glass (1973), and the relationship

between light intensity and reaction distance. In some cases these additions will be necessary to explain position choice behavior - such as why fish often move into low velocity resting positions at night (Kalleberg 1958; Edmundson et al. 1968), when the abundance of invertebrate drift is greatest (Hughes and Dill in prep.).

Incorporating information about the fish's internal state will also be necessary to predict position choice is some situations. For example, fish that become satiated and cease feeding should move to low velocity resting positions, and there is evidence that increased hunger causes fish to move into faster water (Huntingford et al. 1988). A dynamic programming version (Mangel and Clark 1988) of the model might be the best way to include the influence of the fish's internal state on its decision making and position choice.

To explain some aspects of position choice and feeding behavior it may be necessary to alter some of the model's central ideas. For example, we assume attack speed ($VMAX$) to be the fish's maximum sustainable swimming speed, but in fact it is controlled by the fish and may be slower than this, or as high as maximum burst speed. We also constrain the fish to catch prey upstream of a line perpendicular to the current, whereas real fish may intercept prey further downstream. In reality we suspect that solitary grayling choose an attack speed and interception trajectory that minimize the cost of prey capture, and that they pursue all prey large enough to offset capture cost (see Godin and Rangley (1989) for further discussion). In future, similar ideas could be used to explain both position choice and prey capture behavior with a single model

Chapter 2

Ranking of feeding positions by drift-feeding Arctic grayling in dominance hierarchies [1]

Abstract

Field experiments in the pools of a mountain stream demonstrated that Arctic grayling rank feeding positions according to desirability, and that competition sorts fish so that the dominance rank of each individual matches the rank desirability of its position. Groups containing the same number of fish always occupied the same set of positions, and positions were added (in reverse order of desirability) as group size was increased. There was an almost perfect correlation between the dominance rank (measured as fish length) of each fish and the rank desirability of its position, suggesting that competition sorts fish among positions. This conclusion was strengthened by the results of sequential removal experiments in which the dominant fish was removed at the end of each day; after each removal the remaining fish almost always moved into positions previously occupied by fish immediately above them in the dominance hierarchy.

[1] Submitted for publication to the Canadian Journal of Fisheries and Aquatic Sciences.

Introduction

Drift-feeding stream salmonids that select feeding positions in order to maximize their net energy intake (NEI) rate should rank the desirability of feeding positions on the same basis. In addition, competition for profitable positions should sort the members of a dominance hierarchy so that the social rank of each fish corresponds to the rank desirability of its position. This process of ranking and sorting should result in a definite relationship between the layout of the stream habitat and fish distribution pattern; this is because bottom topography and the pattern of current flow play a large part in determining the potential NEI at available positions (Chapter 1; Chapter 3).

These ideas, first expressed by Newman (1956), and supported by Vascotto and Morrow (1973), provide an appealing explanation of the processes that determine the distribution pattern of fish in a dominance hierarchy, but they have been challenged by other field studies. In fact both Jenkins (1969) and Bachman (1984) concluded that sorting of fish among ranked positions was not important in determining fish distribution patterns. This is despite the fact that Jenkins found brown trout *(Salmo trutta)* and rainbow trout and *(Oncorhynchus mykiss)* ranked one position as being more desirable than all the alternative positions, and that the dominant fish in the hierarchy occupied and defended this position. Laboratory studies such as those by Chapman (1962) and Fausch (1984) have been more supportive of Newman's ideas. For example, Fausch showed that the dominance rank of juvenile coho salmon *(O. kisutch)* was closely correlated with predicted NEI at their positions, and with growth rate; this result is consistent with the

hypothesis that fish are sorting themselves among positions ranked on the basis of NEI.

In this work I describe field experiments, using Arctic grayling *(Thymallus arcticus)*, which test Newman's hypothesis that fish rank the desirability of feeding positions, and the closely related hypothesis that competition sorts fish so that the dominance rank of each individual matches the rank desirability of its position.

Methods

To determine if Arctic grayling sort themselves between ranked positions, I conducted position choice experiments in two pools of Twelvemile Creek, a small mountain stream in interior Alaska, during the summer of 1987. Descriptions of Twelvemile Creek, and the methods used in position choice experiments involving a single fish, are given in Chapter 1. In this section I describe the additional techniques used to record position choice in this study, where up to four fish at a time were observed in a pool. I then describe experimental design and the logic used to interpret the results.

Experimental Techniques

To help identify individuals I attached a small colored bird band to the front of each fish's dorsal fin. To avoid the possibility of using fish in more than one experiment each fish was also marked with a small upper caudal finclip.

Arctic grayling are a rugged and cooperative fish - minutes after introduction into a pool, individuals begin to compete for positions and feed. Excellent accounts

of the behaviour involved in this competition are given by Vascotto (1970), Vascotto and Morrow (1973), and Kratt and Smith (1979). Dominance relationships are established quickly - in a two-fish group I have seen the process completed in less than an hour. In four-fish groups it takes longer but usually less than 24 hours. Once dominance relationships are established, social interactions are infrequent and the pattern of distribution is typically stable; individuals spend most of the day feeding from a single position, or from one of a tightly clustered group of positions. For the purposes of this paper, each of these clusters is treated as a single position. This behavior makes it possible to record the distribution pattern of fish the day following an experimental manipulation of a pool's fish population. Position choice of each fish was recorded two or three times during the course of a day at intervals of about six hours. A considerable amount of time was spent observing the fish to confirm the stability of the recorded distribution patterns.

Experimental Design

I used "group size" experiments and "sequential removal" experiments, to test the hypothesis that competition sorts fish between ranked positions. Two pools were used for these experiments - Yellow Flower Pool and Bedrock Pool. The lengths of fish used in these experiments, their dominance rank, and dates of introduction and observation are given in Table 2.1. I assumed that the dominance rank of fish in a group was directly related to its fork-length (Kratt and Smith 1979); to help ensure this I made sure there was a significant difference in length between individuals in each group. Observations of social interactions made during the course of each experiment were used to confirm this assumption, and in only

Table 2.1. Length, dominance rank, date of introduction, and date of observation for fish used in group size experiments in Yellow Flower Pool and Bedrock Pool. Four solitary fish, two groups of two fish, and two groups of four fish were observed in each pool. Some fish swam into the pools between experiments and these are termed "natural residents". The 1st four-fish group from each pool was also used in the sequential removal experiment; otherwise, no individual was used/observed more than once.

	Fork length (mm)	Dominance rank	Date introduced	Date observed
Yellow Flower Pool				
1st Solitary fish	240	1	Natural resident	29 July
2nd Solitary fish	300	1	6 August	7 August
3rd Solitary fish	210	1	8 August	9 August
4th Solitary fish	180	1	9 August	10 August
1st Two-fish group	270	1	19 July	20 July
	216	2	Natural resident	20 July
2nd Two-fish group	260	1	20 August	22 August
	225	2	Natural resident	22 August
1st Four-fish group	260	1	Natural resident	3 August
	225[a]	2	Natural resident	3 August
	240	3	Natural resident	3 August
	205	4	Natural resident	3 August
2nd Four-fish group	260	1	10 August	17 August
	210	2	10 August	17 August
	180	3	13 August	17 August
	155	4	13 August	17 August

Continued...

Table 2.1 continued.

	Fork length (mm)	Dominance rank	Date introduced	Date observed
Bedrock Pool				
1st Solitary fish	280	1	Natural resident	19 July
2nd Solitary fish	240	1	Natural resident	23 July
3rd Solitary fish	250	1	Natural resident	5 August
4th Solitary fish	195	1	6 August	7 August
1st Two-fish group	270	1	Natural resident	3 August
	230	2	Natural resident	3 August
2nd Two-fish group	285	1	Natural resident	28 July
	220	2	Natural resident	28 July
1st Four-fish group	285	1	8 August	9 August
	240	2	8 August	9 August
	225	3	8 August	9 August
	195	4	8 August	9 August
2nd Four-fish group	285	1	20 August	23 August
	230	2	20 August	23 August
	190	3	20 August	23 August
	170	4	20 August	23 August

[a] This was the only fish observed to be dominant over an individual larger than itself.

one case was a smaller fish observed to dominate a larger individual (see Table 2.1).

In the group size experiments, I recorded the distribution pattern adopted by groups of one, two, or four fish. Four solitary fish, two groups of two fish, and two groups of four fish were observed in each pool.

The first four-fish groups used in the group size experiments were also used in the sequential removal experiments, one group in each pool. In these experiments, I removed the dominant fish at the end of each observation day, so that groups of four, three, two and one fish were observed on consecutive days.

Logic of Analysis

If Arctic grayling rank feeding positions according to desirability, I expected positions to be added (in reverse order of desirability) as group size was increased from one to four fish. It follows that groups containing the same number of fish should use the same set of positions. If these predictions are met, then the rank desirability of each position can be determined - it is equal to the number of fish that must be added to the pool before that position is occupied.

If competition sorts fish until the dominance rank of each individual matches the rank desirability of its position, I expected a one-to-one correspondence between the dominance rank of each fish and the rank desirability of its position. I tested for such a correlation using the results of the group size experiments. The sequential removal experiment should also reveal how competition sorts fish between positions; after each removal I expected the remaining fish to move

into the positions previously occupied by the fish immediately above them in the dominance hierarchy.

Results

Ranking of positions

The hypothesis that Arctic grayling rank feeding position according to desirability was strongly supported by results of both group size (Fig. 2.1) and sequential removal experiments (Fig. 2.2). The prediction that positions would be added as group size was increased from one to four fish, and the prediction that groups of the same size would use the same set of positions, were met in almost all cases. Using these results it was possible to determine the rank desirability of the first four feeding positions in Yellow Flower Pool and the first three positions in Bedrock Pool (as shown in Fig. 2.2). The exception to these results were the smallest fish in the four-fish groups observed in Bedrock Pool. Both these fish roamed from one position to another, never settling on one position for long and rarely feeding.

Sorting between positions

The hypothesis that competition sorts fish between positions until the dominance rank of each fish equals the rank desirability of its position was also strongly supported. Using results from the group size experiments I found an almost perfect correlation between the dominance rank of a fish and the rank desirability of its position ($P < 0.001$ using Spearman's Rho; $n=32$). In the

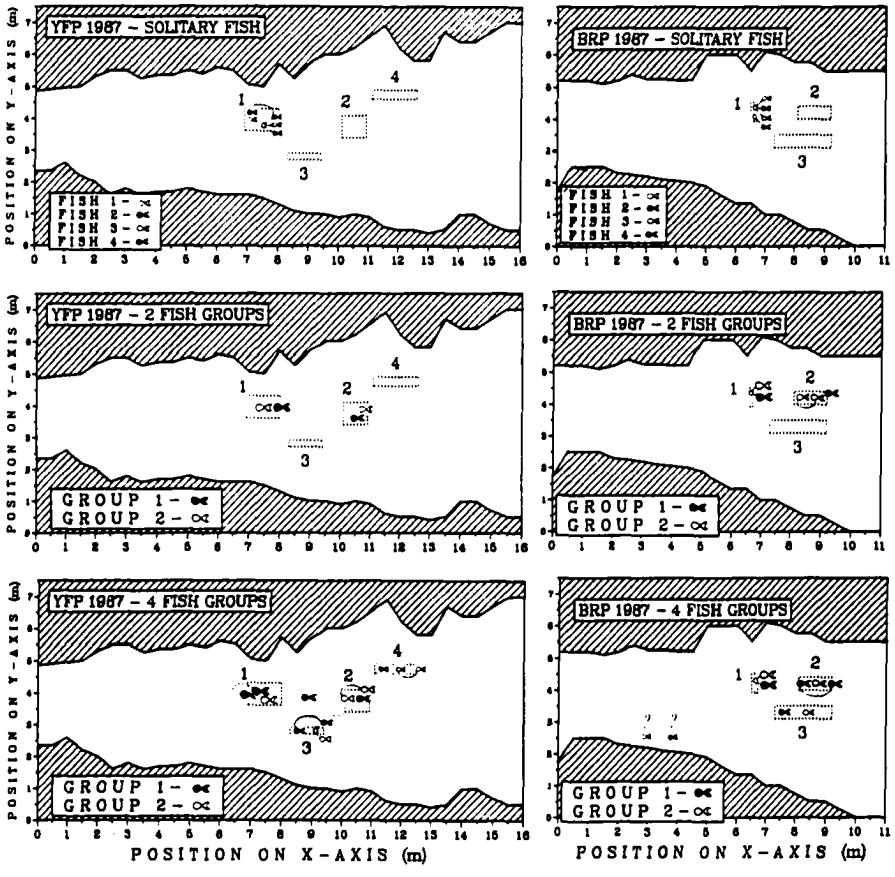
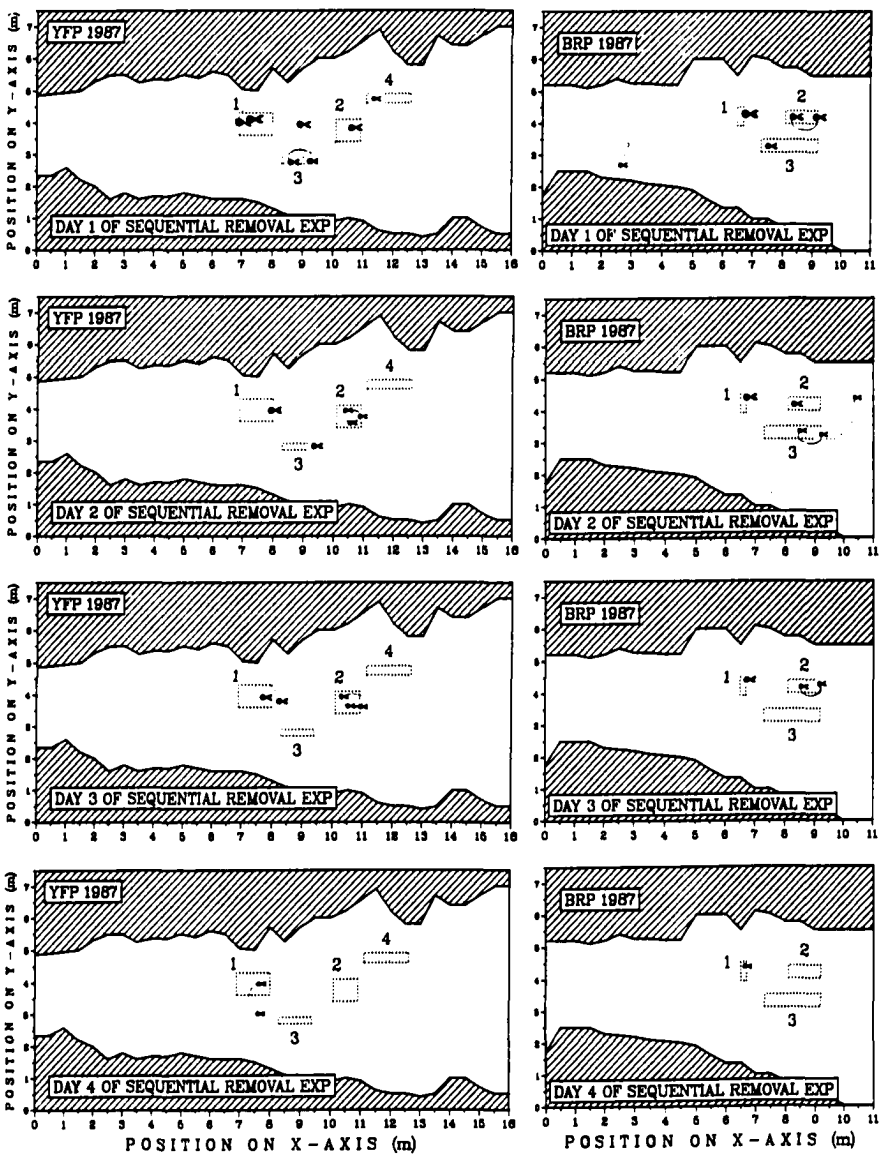


Fig. 2.1. Results of the group size experiments for Yellow Flower Pool (YFP 1987) and Bedrock Pool (BRP 1987). The location of the positions chosen by fish are shown by the symbols and symbol size indicates dominance rank. Curved solid lines connect alternative positions regularly used by the same fish. Curved dashed lines connect primary positions with positions that were rarely used. The question marks over the smallest fish in the four fish groups observed in Bedrock Pool indicate that these fish never settled on a feeding position. The numbered boxes show the location and rank desirability of each position.

Fig. 2.2. Results of the sequential removal experiments for Yellow Flower Pool (YFP 1987) and Bedrock Pool (BRP 1987), showing the positions occupied by the original group of four fish, and by progressively smaller groups on subsequent days of the experiment. The location of the positions chosen by fish are shown by the symbols and symbol size indicates dominance rank. Curved solid lines connect alternative positions regularly used by the same fish. Curved dashed lines connect primary positions with positions that were rarely used. The question mark over the smallest fish on the first day of the experiment in Bedrock Pool indicates that this fish never settled on a feeding position. The numbered boxes show the location and rank desirability of each position.



sequential removal experiment the prediction that, following each removal, fish would move into the positions previously occupied by fish immediately above them in the hierarchy was matched in Bedrock Pool and closely matched in Yellow Flower Pool (Fig. 2.2; Table 2.2).

Discussion

The results of this study demonstrate that Arctic grayling rank feeding positions according to desirability, and that competition sorts fish so that the dominance rank of each individual matches the rank desirability of its position.

The behavior of the smallest fish in each of the four-fish groups observed in Bedrock Pool is the only result that doesn't easily fit into this explanation. Apparently neither of these fish could settle on a single "fourth ranked" position. Perhaps the physical uniformity of the positions available to them meant that there was no real basis for ranking. Alternatively, it is possible that, from the fishes' point of view, there was no fourth ranked position in the pool, and that these fish were "refugees" unable to find a position in the pool but prevented from leaving by the blocknets.

The experiments in this study support the conclusions that Newman (1956), Vascotto and Morrow (1973), and Fausch (1984) drew from their studies on distribution patterns of drift-feeding stream salmonids. However these results do not agree with the conclusions of Jenkins (1969) or Bachman (1984); they found little or no evidence for the sorting of fish between ranked positions and both argue that this process is unimportant in determining distribution patterns (even though Jenkins' found that the dominant fish did occupy a top ranked position).

Table 2.2. Rank desirability of positions occupied by fish in Yellow Flower Pool and Bedrock Pool on the four consecutive days of the sequential removal experiments. Fish are listed in order of dominance rank and the dominant fish was removed at the end of each observation day. These are the 1st four-fish groups used in the group size experiments (Table 2.1). The first day of each sequential removal experiment was also the observation day for the group size experiment.

	Fork length (mm)	Day 1	Day 2	Day 3	Day 4
Yellow Flower Pool	260	1			
	225	2	1		
	240	3	3	1	
	205	4	2	2	1
Bedrock Pool	285	1			
	240	2	1		
	225	3	2	1	
	195	?	3	2	1

How can these conflicting conclusions be explained? One possibility is that the fish in Jenkins' and Bachman's studies did not rank positions because all positions provided equal NEI. This is the explanation that the authors themselves favor. Habitat uniformity could account for the lack of ranking in Jenkins' study, because most of the positions were in riffles, and probably shared similar physical characteristics. However the habitat map in Bachman's study shows considerable differences in depth (and presumably velocity) between different feeding positions and so this habitat uniformity argument probably can't explain the apparent absence of ranking. Bachman's study revealed that individual brown trout were sometimes faithful to the same feeding positions for several years; perhaps this site fidelity (the function of which is unknown) is of overriding importance in determining the distribution pattern of these fish.

This study shows that the sorting of fish among ranked positions can explain the distribution patterns adopted by hierarchies of drift-feeding stream fishes. In Chapter 3 I investigate the processes that determine the location and ranking of these positions. If these processes were understood we would have a complete explanation for the distribution patterns that these fish adopt.

CHAPTER 3

Position Choice by Drift-Feeding Salmonids in Dominance Hierarchies: Model and Test for Arctic Grayling in Subarctic Mountain Streams, Interior Alaska [1]

Abstract

This study describes a model to predict position choice by each individual in a dominance hierarchy of drift-feeding stream salmonids; this is an extension of Hughes and Dill's model (Chapter 1) of position choice by solitary fish. It includes the effect that prey consumption, lateral diffusion, and entry of invertebrates into the drift have on the density of prey downstream of feeding fish, and the restrictions that dominant fish place on freedom of choice by their subordinates. The model assumes that each fish chooses the most profitable position that its rank in the hierarchy will allow. There was an encouraging match between the distribution patterns predicted by the model and the distribution patterns actually adopted by Arctic grayling *(Thymallus arcticus)* in two pools of a mountain stream. This result suggests that Arctic grayling locate and rank positions based on their profitability. The predictions of simplified versions of the model, and the location of positions in relation to bottom topography and current flow, show that the physical habitat forms the template for distribution patterns by determining the location and ranking of the most profitable positions.

[1] Submitted for publication to the Canadian Journal of Fisheries and Aquatic Sciences.

Introduction

Several studies have shown that drift-feeding salmonids in dominance hierarchies rank feeding positions according to desirability, and that competition sorts fish so the dominance rank of each individual matches the rank desirability of its position (Newman 1956; Vascotto and Morrow 1973; Fausch 1984; Chapter 2). If we understood the processes that determine the location and ranking of these positions we could explain the distribution patterns adopted by these fish. In this study I present a foraging model that shows how physical habitat provides the template for these distribution patterns by determining the location and ranking of the most profitable feeding positions.

Previous work has shown the importance of social behaviour in spacing out groups of drift-feeding salmonids (Newman 1956; Kalleberg 1958, Chapman 1962; Jenkins 1969; Slaney and Northcote 1974; Dill et al. 1981; Bachman 1984; Grant and Kramer 1990) but much less is known about the processes that determine the location and ranking of the positions these fish use. To date, Fausch (1984) provides the most complete account. His study suggests that coho salmon *(Oncorhynchus kisutch)* may locate and rank positions based on potential net energy intake (NEI) rate, explaining the adaptive value of position choice. His use of a foraging model also helps to explain how water velocity and prey density determine NEI although his model cannot be used to predict the location and ranking of positions (see Chapter 1 for more discussion of Fausch's model).

In this work, I modify Hughes and Dill's model (Chapter 1), for position choice by solitary fish, to predict the location and ranking of the positions used

in hierarchies containing two or more fish. I have include the effect that prey consumption, lateral diffusion, and entry of invertebrates into the drift, have on prey density downstream of a feeding fish - and the restrictions that dominant fish place on freedom of choice by their subordinates. To test the hypothesis that fish locate and rank position on the basis of potential NEI, I compare the location and ranking of positions predicted by the model to the location and ranking of the positions actually selected by Arctic grayling *(Thymallus arcticus)* in the pools of a mountain stream. To examine the effect of the individual processes in the model, I compare the predictions of the full model to the predictions of reduced models, from which the effect of a single process had been removed. Finally, to determine the way in which the physical habitat acts as the template for fish distribution, I examine the relationship between bottom topography and current flow, and the location of observed and predicted positions.

In one sense, I think that the distribution pattern adopted by fish in a pool is the consequence of the bottom topography and the pattern of current flow; and yet in another sense it is the result of each fish selecting the position that maximizes its NEI. The purpose of this work is to show how these two answers are linked, by describing the way physical habitat determines the location and ranking of profitable positions.

Methods

First I explain how I expanded Hughes and Dill's model (Chapter 1), adapting it to predict the positions occupied by each fish in a dominance hierarchy. Next I describe how this model was used to predict the distribution pattern of Arctic

grayling in the pools of a subarctic mountain stream, and how these predictions were tested. Third, I explain how I ran reduced versions of the model to examine the influence of each of its components on the predicted distribution pattern. Finally I describe how I evaluated the relationship between the location and ranking of positions and the pool habitat.

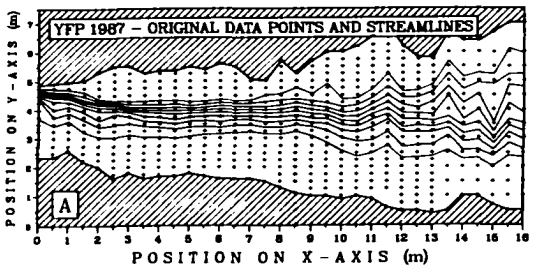
A: The Model

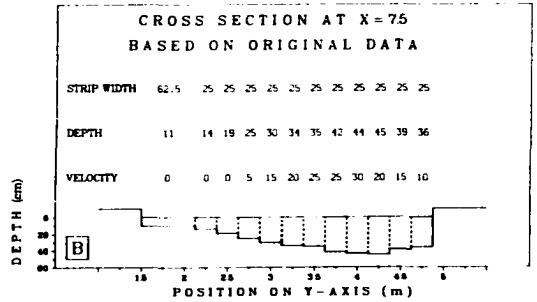
Habitat description

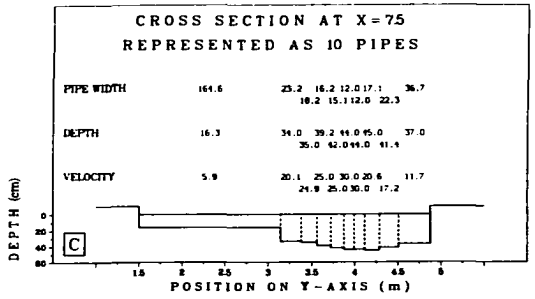
Hughes and Dill (Chapter 1) describe the habitat using a series of cross sections, each composed of a variable number of vertical strips. While this description is convenient when predicting the position of a single fish, it is not so suitable for a model that predicts the distribution of several fish. This is because of the difficulties it creates when modeling processes which are dependent on the pattern of water flow - such as turbulent mixing of invertebrates downstream of a feeding fish. To make modeling of these processes more tractable I process the original cross section data to provide a new description of the habitat in which the pool is described as a number of "pipes" separated by "streamlines" (Vogel 1983). The methods involved in this transformation are described in Fig. 3.1. Although the series of cross sections produced by this transformation are now defined differently than by Hughes and Dill (Chapter 1), the methods they used to calculate capture areas can be used without modification.

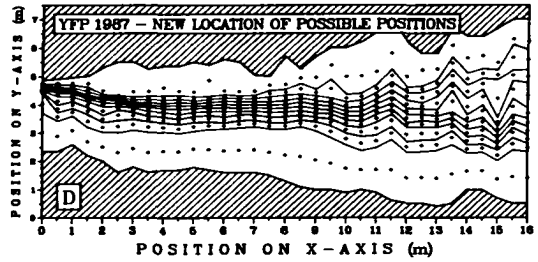
For clarity, I use 10 pipes to describe the pool while illustrating how the model works in this section. In the simulations to predict the distribution pattern of

Fig. 3.1. Showing how the original depth and velocity measurements are transformed to describe the pool as a series of "pipes" separated by imaginary vertical walls or "streamlines". In panel "A" crosses mark the location at which depth and velocity measurements were taken in one of the study pools (Yellow Flower Pool 1987); flow is from left to right. There are 33 cross sections and measurements were taken at 0.25 m or 0.5 m intervals along each cross section. The nine streamlines drawn through these points divide the pool into ten pipes, each pipe carrying one tenth of the stream discharge. To calculate the path of these streamlines each cross section is initially visualized as a series of strips centered on the location at which water depth and velocity were measured and characterised by these two measurements (as in Chapter 1). The 16th cross section (X coordinate = 7.5 m) is represented in this way in panel "B". The Y coordinate at which each of the nine streamlines must intersect the cross section, in order to divide it into ten pipes with equal discharge, is then calculated. Once these coordinates have been determined for all the cross sections, the path of each streamline is known. Next, a new description for each cross section is developed in which pipes replace strips (panel "C"). Each pipe is characterised by water depth and velocity and bounded by the streamlines. The water depth in each pipe at each cross section is calculated as the weighted mean depth of the original strips that contributed to that pipe. The water velocity in each pipe at each cross section is calculated from pipe width, pipe depth, and pipe discharge. Finally the coordinates of possible feeding positions are calculated. These positions are located along each of the 33 cross sections, with one position in the center of each pipe (panel "D").









Arctic grayling I actually used 25 pipes; this number provides enough positions to cover the area actually used by the fish in the study pools, while still allowing a reasonable run time on the computer.

Spatial variation in drift concentration

Hughes and Dill assumed that invertebrate drift concentration was the same at all points in a pool. This is probably a fair assumption to make when predicting position choice by a single fish but not when predicting the position choice of additional fish because a feeding fish will influence the density of prey further downstream. To predict position choice by additional fish it is necessary to keep track of this spatial variation in drift density. To do this, I assigned a value between 0 and 1, for each prey size class, to each of the possible positions. This number represents the density of prey at that position as a proportion of the unexploited prey abundance or $PPC_{cs,p,i}$. The subscript cs represents the number of the cross section containing the position, counting from the head of the pool; p is the number of the pipe containing the position, counting from the left bank looking upstream; i is the size class of prey ($i = 1,...,3$; after Hughes and Dill, Chapter 1). $PPC_{cs,p,i}$ can be converted to the actual prey density by multiplication with the unexploited drift density for prey in size class i or PC_i (Chapter 1).

Drift removal by feeding fish

Drift-feeding fish remove invertebrates and this influences the density of drift downstream. The method I used to model this removal is explained in Fig. 3.2. I have assumed that fish are 100% efficient at catching prey that pass through their capture area. This assumption is supported by the work of Wankowski (1981) and Dunbrack and Dill (1984) which demonstrate very high capture rates out to the edge of a fish's capture area, and then a sharp step-like decline. However, capture rates could be significantly less than one in some situations, and this could easily be accounted for within the framework described in Fig. 3.2.

Lateral diffusion of invertebrates

The variation in prey abundance between neighbouring pipes produced by a feeding fish will not persist unchanged for the length of the pool because lateral diffusion will even out the differences. Ciborowski (1983) has shown how the rate of lateral diffusion can be estimated using S_{LD} - the standard deviation of the lateral distance travelled by invertebrates, released from a single point, after travelling a known distance downstream. The way I use this concept to model the effect of lateral diffusion on prey density downstream of a feeding fish is described in Fig. 3.3; Ciborowski's equation for S_{LD} is given in Table 3.1.

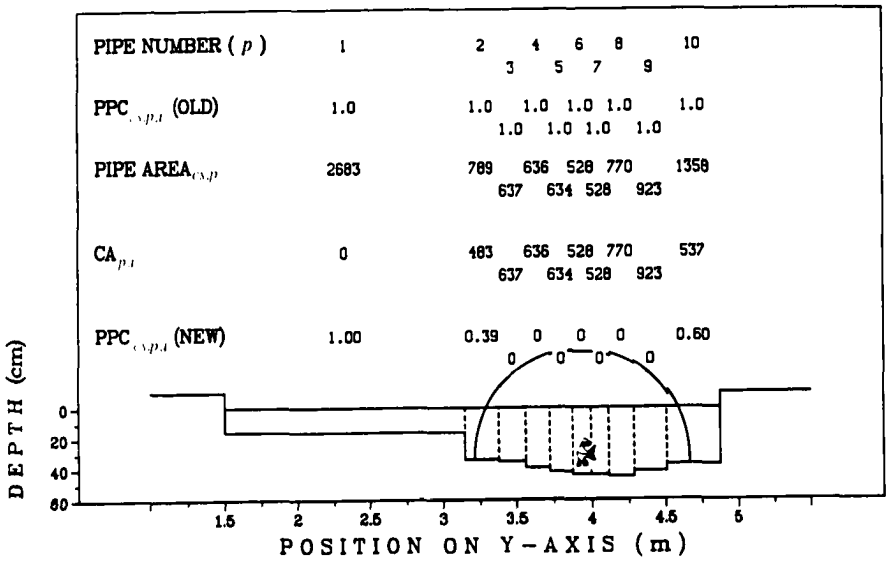


Fig. 3.2. Calculating the effect of fish feeding on prey abundance. The fish (26 cm fork length) is holding station in pipe 6 on cross section 33 (X coordinate = 7.5 m). Calculation of its influence on the abundance of prey in size class i = 3 is illustrated. The jagged semi-circle shows the maximum capture distance ($MCD_{p,i}$) of the fish to prey in this size class (Chapter 1 describe how to calculate $MCD_{p,i}$). The capture area for prey in each of the pipes ($CA_{p,i}$) is the overlap of this semicircle with pipe p. Once the $CA_{p,i}$ are known the effect of the fish on the concentration of prey in pipe tube can be is calculated as -

$$PPC_{cs,p,i}(NEW) = [(PIPEAREA_{cs,p} - CA_{p,i})/PIPEAREA_{cs,p}] \cdot PPC_{cs,p,i}(OLD)$$

where $PIPEAREA_{cs,p}$ are the cross sectional areas of the pipes at this cross section, $PPC_{cs,p,i}(OLD)$ is the proportional prey abundance in the pipes at this cross section before the effect of the fish's feeding has been calculated, and $PPC_{cs,p,i}(NEW)$ are the values after the effect of feeding has been calculated. In this example the $PPC_{cs,p,i}(OLD)$ all equal 1 (indicating 100% of unexploited prey concentration) but the equation works for any values of $PPC_{cs,p,i}(OLD)$.

Fig. 3.3. Calculating the effect of lateral diffusion on the distribution of drifting invertebrates in size class i = 3, as they travel the 0.5 m from one cross section to the next. For the purposes of this calculation, the widths of all pipes are assumed to be equal and uniform. Median pipe width was used; this is 23 cm when 10 pipes are used to describe Yellow Flower Pool (1987). The dispersion of invertebrates in each of the donor pipes at cross section 33 (X coordinate = 7.5 m) among the recipient pipes at cross section 34 (X coordinate = 8.0 m) is calculated using the standard deviation of the lateral distance travelled by invertebrates as they move 0.5 m downstream (S_{LD}) and the standard normal distribution. S_{LD} was calculated using Ciborowski's (1983) equation (Table 3.1) and was 22 cm in this pool. Panel "A" shows how the $PPC_{ce,p,i}$ for pipe 2 is redistributed as water flows from cross section 33 to cross section 34. The distance from the center of pipe 2 to its boundaries with neighbouring pipes is 11.5 cm, and the standard normal distribution shows that if S_{LD} = 22 then 38% of the prey that were in pipe 2 at cross section 33 will remain in this pipe at cross section 34. This means that pipe 2 at cross section 33 will contribute $0.38 \cdot PPC_{33,2,3} = 0.38 \cdot 0.39 = 0.15$ to the final value of $PPC_{34,2,3}$. The same logic, using the distance between the center of the donor pipe and the neighbouring pipe boundaries, is used to apportion the entire $PPC_{33,2,3}$ among the pipes at cross section 34. The results of this calculation are shown in panel "A"; the contribution of 0.02, "suspended" over pipe 1, shows how the edges of the cross section are treated like a mirror "reflecting" drifting invertebrates back towards the center of the current (as suggested by Smith 1975); the "suspended" 0.02 is added to the value of 0.10 to give the total contribution of $PPC_{33,2,3}$ to $PPC_{34,1,3}$. This redistribution of $PPC_{ce,p,i}$, from donor pipe to recipient pipes, is repeated for all the pipes along the donor cross section. The contributions to each pipe at the recipient cross section are then summed to give the final result (panel "B"). Notice that the $PPC_{ce,p,i}$ at cross section 33 sum up to the same amount as the $PPC_{ce,p,i}$ at cross section 34 showing how these calculations redistribute prey but do not increase or decrease the total number of invertebrates in the drift.

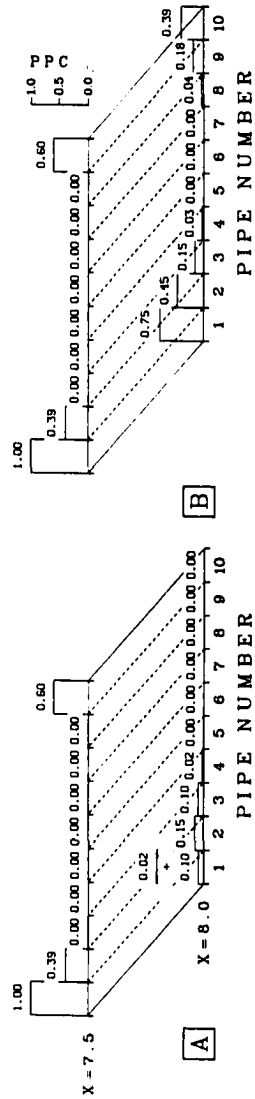


Table 3.1. Equations used to estimate the standard deviation of lateral diffusion for drifting invertebrates (SD_{LD}), and the increment in drift concentration due to resuspension of invertebrates from the stream bed ($IR_{cs,p,i}$) as water travels 0.5 m from one cross-section to the next. The equation for SD_{LD} is from Ciborowski (1983), and I developed the equation for ($IR_{cs,p,i}$) from the equations to predict drift density downstream of a drift net blockage given in McLay (1970) and Elliott (1971). Both equations are parameterized using the values given by Ciborowski (1983) for live *Baetis tricaudatus* (spring). V_{MEDIAN} is the median water velocity in the pool. $PPC_{cs,p,i}(OLD)$ is the concentration of prey in size-class i (as a proportion of unexploited concentration) in pipe p at cross-section cs prior to adding the effect of resuspension of drift from the stream bed. $V_{cs,p}$ is the water velocity in pipe p at cross section cs.

Parameter	Units	Equation
SD_{LD}	cm	$SD_{LD} = -0.560 + 0.659 \cdot \sqrt{0.5} + 0.0103 \cdot V_{MEDIAN}$
$IR_{cs,p,i}$	None	$IR_{cs,p,i} = (1 - e^{-R \cdot 0.5}) \cdot (1 - PPC_{cs,p,i}(OLD))$ where $R = 8.01 \cdot V_{cs,p}^{-1.07}$

Table 3.2. Median pipe width, median water velocity, and standard deviation of lateral diffusion of invertebrates (SD_{LD}) for Yellow Flower Pool and Bedrock Pool when 25 pipes are used to describe each pool. SD_{LD} was calculated using Ciborowski's equation from Table 3.1.

	Median pipe width (cm)	Median water velocity ($cm \cdot s^{-1}$)	SD_{LD} (cm)
Yellow Flower Pool	8.5	30	22
Bedrock Pool	7.5	45	37

Entry of invertebrates into the drift

Lateral diffusion is not the only process that influences the density of invertebrates downstream of a feeding fish; the entry of invertebrates into the drift will increase drift density when $PPC_{ca,p,i} < 1$, and the net movement of invertebrates into the drift will continue until $PPC_{ca,p,i} = 1$. The dynamics of this process have been expressed mathematically by McLay (1970) and Elliott (1971). Based on their equations I developed a relationship for the change in prey abundance caused by re-suspension of drift as the water in a pipe passes from one cross section to the next (Table 3.1). I used this relationship to model the way that entry of invertebrates into the drift influence prey abundance downstream of a feeding fish (Fig. 3.4). The combined effect of fish feeding, lateral diffusion, and drift re-suspension on the density of a single size class of prey downstream of a feeding fish is shown in Fig. 3.5.

Social restrictions on position choice

Dominant fish restrict the positions available to their subordinates and this process is very important in determining the distribution pattern of fish in a dominance hierarchy. It means that a fish is not necessarily free to select the position that maximizes its net energy intake but has to settle for the best position outside of the "restricted area" imposed by dominant fish.

While several studies have determined the size and shape of the areas defended by juvenile stream salmonids in territorial mosaics (Kalleberg 1958; Slaney and Northcote 1974; Dill et al. 1981) there is no comparable work on larger fish

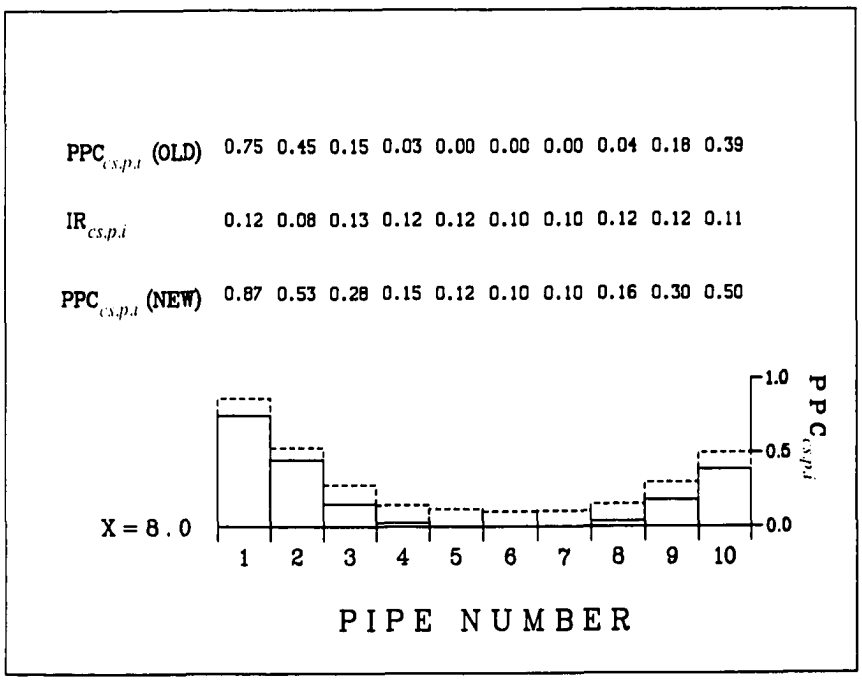


Fig. 3.4. Modeling the effect of re-suspension of invertebrates from the stream bed on prey abundance. Cross section 34 (X coordinate = 8.0 m) is shown and these calculation begin where the calculations of Fig. 3.3 left off. The effect of drift re-suspension on prey abundance at a cross section is determined after the calculations of lateral diffusion and downstream transport from the cross section immediately upstream are complete, but before the effect of lateral diffusion downstream to the next cross section is calculated. I used my adaptation of McLay's (1970) and Elliott's (1971) equations (Table 3.1) to calculate the increment in $PPC_{cs,p,i}$ due to re-suspension ($IR_{cs,p,i}$) as the water travels the 0.5 m from cross section 33 to cross section 34. The $PPC_{cs,p,i}$ ($PPC_{cs,p,i}(OLD)$ in this figure) and water velocity in the recipient pipe are used to calculate this increment, rather than values from the donor pipe. This avoids calculation of final values of $PPC_{cs,p,i}$ ($PPC_{cs,p,i}(NEW)$ in this figure) larger than 1. The $IR_{cs,p,i}$ is added to $PPC_{cs,p,i}(OLD)$ to give $PPC_{cs,p,i}(NEW)$. The solid bars show $PPC_{cs,p,i}(OLD)$, the increment shown by the dashed bars $IR_{cs,p,i}$, and the total height of the bars $PPC_{cs,p,i}(NEW)$.

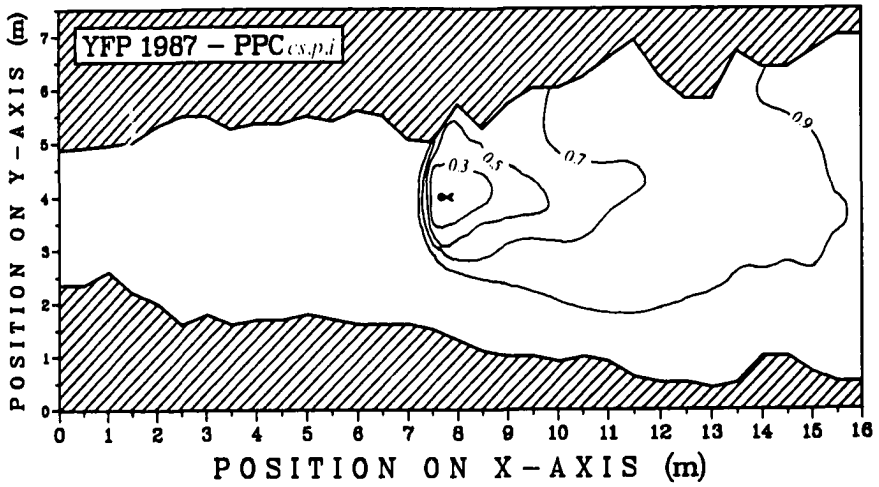


Fig. 3.5. Showing the effect of fish feeding, lateral diffusion, and re-suspension of invertebrates from the stream bed, on the concentration of prey in size class $i = 3$ downstream of a fish (26 cm fork length) feeding in pipe 6 of cross section 33. Prey abundance is expressed as a proportion of the unexploited prey abundance ($PPC_{cs,p,i}$). The spatial variation in abundance of invertebrates will be different for each size class of prey because the reaction distance of the fish depends on prey size (see Chapter 1).

in dominance hierarchies. In addition, my observations of Arctic grayling have convinced me that the territorial mosaic concept which has proved so productive with juvenile salmonids, cannot explain the way that social behavior spaces members in hierarchies made up of adult and sub-adult fish (see Bachman (1984) for further discussion about the utility of the territory concept for larger fish). This lack of any well worked out relationship has led me to develop a set of rules with which to determine the shape of the restricted area, based on my observation of Arctic grayling in the pools of Twelvemile Creek, interior Alaska. These rules, and the logic behind them, are as follows.

The dominant Arctic grayling in a pool is very intolerant of subordinates that attempt to feed at positions upstream of its own, unless the subordinate is considerably to one side of the pipe occupied by the dominant fish. To model this intolerance, I gave the dominant fish in the pool a defended area that extends upstream from its feeding position to the head of the pool, and 156 cm to either side of the center of the stream tube containing its position. This rule prevents a subordinate fish from selecting any position where prey would pass through its reaction field before they passed through the reaction field of the dominant fish (lateral diffusion neglected), because the reaction distance of fish to the largest size class of prey is about 78 cm (Hughes and Dill, Chapter 1).

Like the dominant fish in the hierarchy, the number 2 fish will sometimes swim 4 or 5 m to displace a subordinate that is directly upstream of its own position. However, the number 2 fish is more tolerant than the dominant fish because it will allow subordinates to occupy positions upstream of its own as long as they are more than 60 cm to one side of the pipe occupied by the number 2 fish (see

Figs. 2.1 and 2.2 in Chapter 2). For these reasons I gave the number 2, and lower ranking fish, a defended area extending upstream from their feeding positions to the head of the pool, but only 60 cm to either side of the center of the pipe containing their feeding position. This technique of assigning restricted areas is illustrated in Fig. 3.6.

These rules for determining restricted areas are not as objective as the methods used to model spatial variations in drift concentration, but they do give a reasonable description of Arctic grayling behavior, and at present no independently derived methods are available.

B: Predicting Arctic Grayling Distribution

The position choice of the dominant fish is predicted first, followed by the choices of successively lower ranking fish. Each fish is assigned to the position that the model predicts will maximize its NEI, with the constraint that no fish can occupy the "restricted area" defended by higher ranking individuals. To find this position, predicted NEI is calculated for all possible positions each time a fish is being placed. NEI is calculated almost exactly as described in Chapter 1, except that, in keeping with the modifications and changes in notation described in this paper, their equation (2) for calculation of the fish's gross energy intake rate (GEI) is now more conveniently expressed as:

(1)

$$GEI = \sum_{p=1}^{NPIPES} \sum_{i=1}^{3} CA_{p,i} \cdot V_{ca,p} \cdot PPC_{ca,p,i} \cdot PC_i \cdot PE_i \cdot 3,600/1,000,000$$

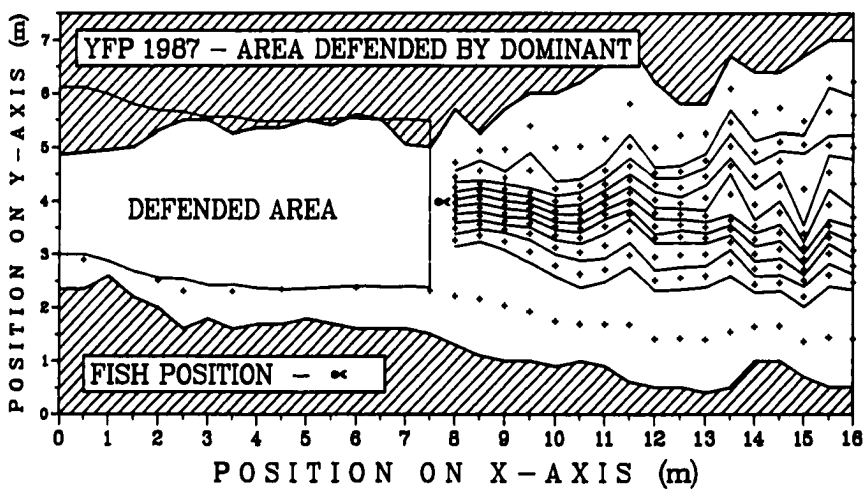


Fig. 3.6. Showing how the area from which a dominant fish excludes its subordinates is described. The dominant fish has a position in pipe 6 on cross section 33. Its defended area extends upstream of this position to the head of the pool, and 156 cm to either side of the center of pipe 6. For lower ranking fish, the defended area only extends 60 cm either side of the pipe containing the fish's feeding position.

where $NPIPES$ is the number of pipes used to describe the pool, $CA_{p,i}$ is the capture area of the fish for prey in size class i in pipe p, $V_{cs,p}$ is the water velocity at pipe p in cross section cs, $PPC_{cs,p,i}$ is the density of prey in length class i at pipe p in cross section cs as a proportion of its unexploited concentration, PC_i is the unexploited prey concentration of prey in size class i, PE_i is the energy content of each prey in length class i, and the 3,600/1,000,000 term is necessary because $CA_{p,i}$ and $V_{cs,p}$ have units of centimeters and seconds while PC_i and GEI have units of meters and hours. NEI is then calculated as $GEI - SC$ where SC is the fish's swimming cost. The necessary definitions, equations, and parameter values for Arctic grayling are given in Chapter 1.

After a fish has been assigned to a position, values of $PPC_{cs,p,i}$ are recalculated for all the positions in the pool, and the area that fish defends is defined, before predicting the position of the next fish. I recalculate $PPC_{cs,p,i}$ by starting at the top of the pool and working downstream, one cross section at a time. When a cross section contains a fish's position the effect of this fish on the density of drift in that cross section is calculated (as described in Fig. 3.2). Next the combined effects of lateral diffusion and re-suspension on $PPC_{cs,p,i}$ are calculated down to and including the next cross section to hold a fish (as described in Figs. 3.3 and 3.4). The effect of this fish on $PPC_{cs,p,i}$ is then calculated and the process is continued to the end of the pool. If there are two or more fish on a single cross section the effect of each of them on $PPC_{cs,p,i}$ is calculated in turn, starting with the highest ranking fish, before continuing downstream.

Testing the model

I tested the model by comparing the distribution patterns it predicted in two pools of Twelvemile Creek (Bedrock Pool 1987 and Yellow Flower Pool 1987) to the distribution patterns actually adopted by Arctic grayling in these pools. Hughes and Dill (Chapter 1) describe Twelvemile Creek and the methods used to map the pool habitat. Values for median pipe width, median water velocity, and the standard deviation of lateral diffusion are given in Table 3.2. The methods used to determine the distribution patterns actually adopted by Arctic grayling in these pools is described Chapter 2. Predictions were made for a group of four fish in Yellow Flower Pool, and three fish in Bedrock Pool. The fork lengths of these fish were, in order of dominance rank: Yellow Flower Pool: 26, 22.5, 24, and 20.5 cm; Bedrock Pool: 28.5, 24, and 22.5 cm. These lengths and ranks correspond to the first four-fish group observed in Yellow Flower Pool, and the largest three fish in the first four-fish group in Bedrock Pool, during the group-size experiments described in Chapter 2.

C: Investigating Individual Processes

To examine the influence individual processes have on the distribution pattern predicted by the model I evaluated versions of the model without the effects of prey capture, lateral diffusion, re-suspension of drift, and restricted areas. Although some of these versions are unrealistic the results of this exercise are helpful in explaining the distribution pattern of fish in a dominance hierarchy.

D: Distribution Patterns and the Physical Habitat

To determine the extent to which the bottom topography of the pool and the pattern of water flow provide the template for fish distribution I examined the distribution of the observed and predicted positions in relation to these habitat features.

Results

Observed vs Predicted Distribution Patterns

The match between predicted and observed patterns of fish distribution is shown in Figs. 3.7 and 3.8. In both pools the predicted distribution matches the observed distribution quite well.

In Yellow Flower Pool, the model accurately predicts the location and ranking of the two most desirable positions in the pool and makes fairly accurate predictions for the third position (predicted positions are a little too close to the center of the current), but is wide of the mark for the fourth position (predicted position is too far downstream and too near the center of the current). In Bedrock Pool, predictions for the first and third positions were accurate and the predictions for the second ranking position were quite accurate when assessed by the method used in Fig. 3.8 (6 out of 11 of the predicted positions lie within the target area) but were more than 1 m too far downstream when assessed by the method used in Fig. 3.7.

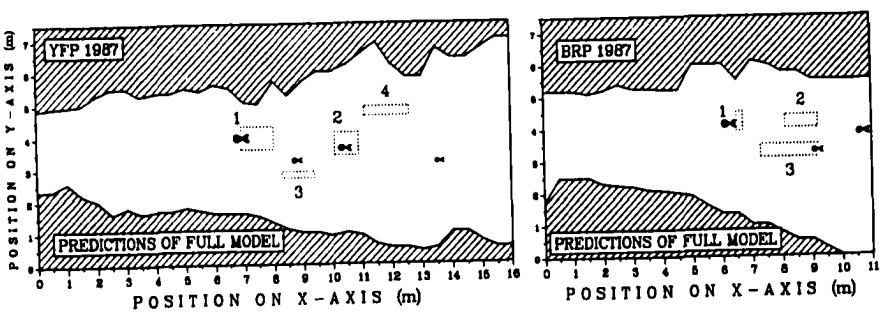
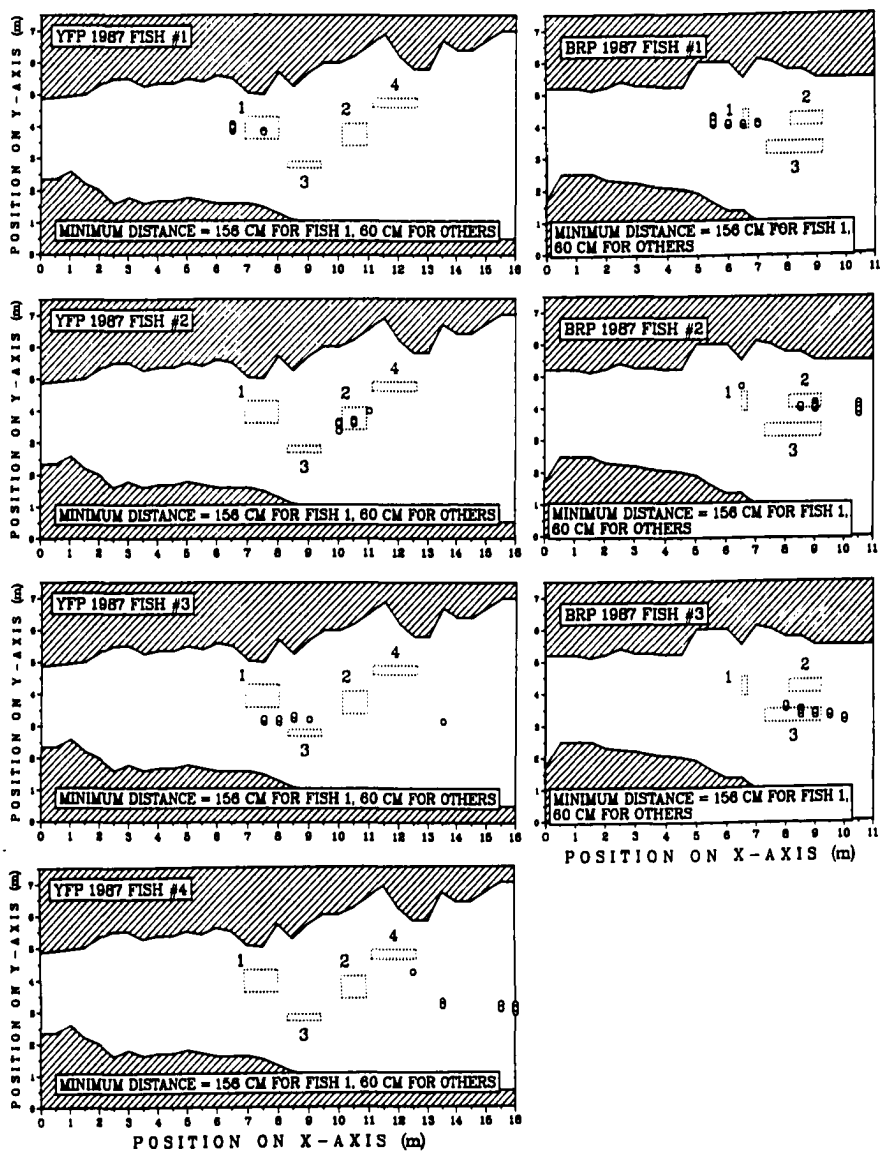


Fig. 3.7. Comparison of the distribution pattern predicted by the model and the distribution pattern actually adopted by the Arctic grayling in Yellow Flower Pool (YFP 1987) and Bedrock Pool (BRP 1987). The predicted positions are indicated by the fish symbols, where symbol size represents dominance rank. The numbered boxes show the location and rank desirability of positions actually used by the fish (Chapter 2). For a perfect match between the predicted and observed results, the largest fish symbol should lie within box 1, the second largest fish in box 2 and so on.

Fig. 3.8. A comparison between the location of the positions that the model ranked in the top 1% (YFP 1987) or 2% (BRP 1987) of all possible positions with the positions actually used by fish. The circles show the location of the predicted positions while the numbered boxes show the location and ranking of positions actually used by the fish (Chapter 2). The results for each fish in the hierarchy are plotted separately. In a perfect match between predictions and observations the predicted positions for fish number 1 should cluster within and around box 1, the predicted positions for fish number 2 should cluster around box 2, and so on.



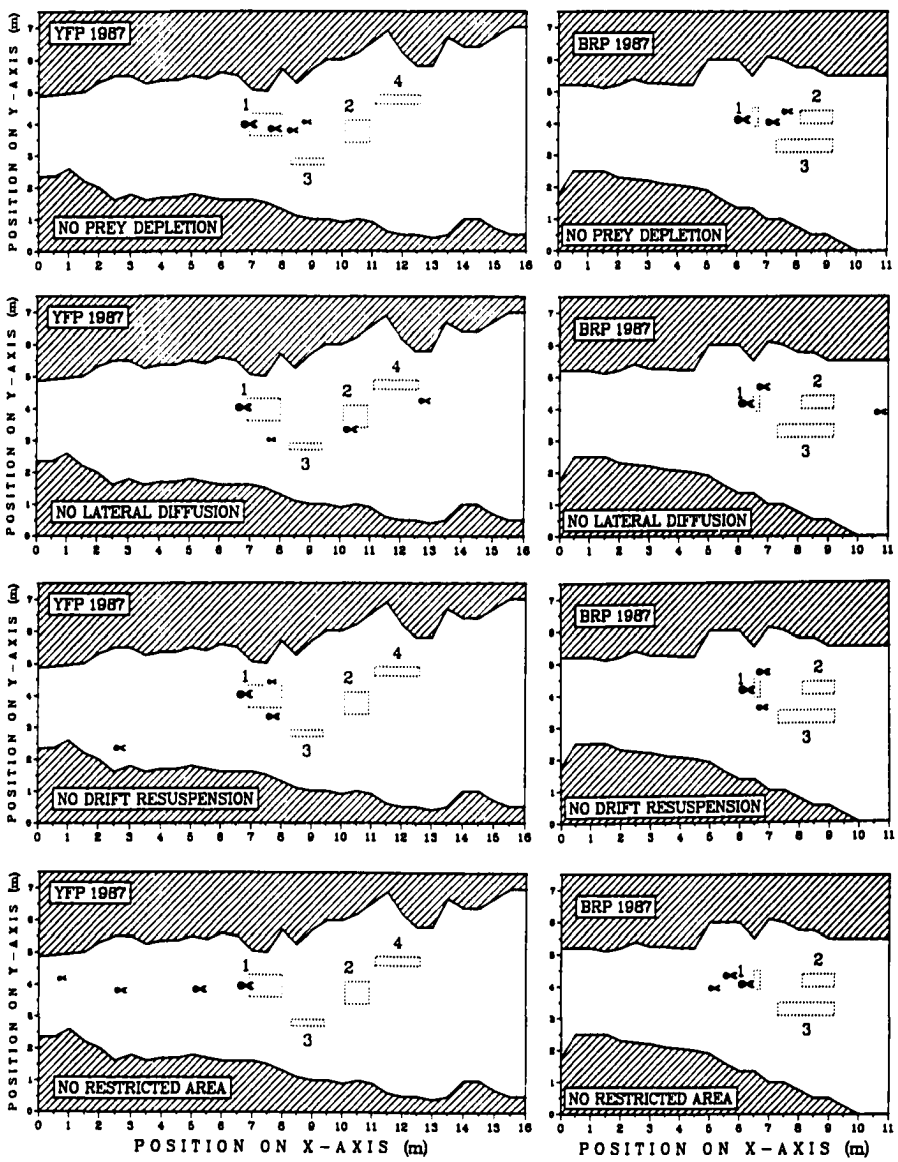
Predictions of Reduced Models

The distribution patterns predicted by the four reduced versions of the model are shown in Fig. 3.9. None of the reduced models made more realistic predictions than the full model and, in most cases, their predictions were much worse. When compared to the full model, each of the reduced versions produced characteristic changes in the predicted distribution pattern. The "no prey depletion" model predicted that each fish would choose a position right on the tail of the fish immediately above it in the dominance hierarchy. Predictions of the "no lateral diffusion" model were most similar to the full model (predictions for Yellow Flower Pool may even have been better than the full model), the main difference was that number 2 fish moved laterally, so that it was longer directly downstream of the number 1 fish. In Yellow Flower Pool the number 3 and number 4 fish also moved to positions further from the center of the current. The "no re-suspension" model predicted that subordinate fish would move to positions further upstream and fan out across the pool. The "no restricted area" model predicted that each fish would choose a position directly upstream of the fish immediately above it in the dominance hierarchy.

Distribution Patterns and the Physical Habitat

The location and ranking of both observed positions and the positions predicted by the full model bear a definite relationship to the bottom topography and current flow in the pool. This fit is made particularly striking by similarities in the physical layout of the two pools; within limits Bedrock Pool looks very much like the upper

Fig. 3.9. Distribution patterns predicted by the four reduced models in Yellow Flower Pool (YFP 1987) and Bedrock Pool (1987). The fish symbols show the predicted positions and the size of the symbol corresponds to dominance rank. The numbered boxes show the location and ranking of positions actually used by Arctic grayling in these two pools (Chapter 2).



11 m of Yellow Flower Pool (Fig. 3.10). In both pools, the top ranked position lies just downstream of the deepest part of the pool in the center of the current. The second ranking position lies directly downstream of the first, also in the center of the current, and in a small depression in the bottom that "buds" off from the main depression. The third ranking position is downstream of the first position, level with or upstream of the second position, and to one side of the main flow. The depth contours show that this position is in a "scallop" in the stream bed on the more gently sloping side of the pool, so that the fish is occupying the deepest water possible given its distance from the center of the current. The streamlines show that there is a distinct lateral component to the flow at these positions. The fourth highest ranking position in Yellow Flower Pool was downstream of all other positions, on the opposite side of the pool from the third position, and in slightly shallower water. Otherwise its physical characteristics were similar to the third ranked position; it too was in a scallop in the stream bed at a position where there was significant lateral flow. Examination of Bedrock Pool suggests that if there were a fourth position it might be at about X = 10.5 m, Y = 5.0 m, which is similar in nature to the fourth position in Yellow Flower Pool. Its intriguing that the third ranking fish in Bedrock Pool did occasionally use a position in this area as an alternative to its usual position (Chapter 2 - day 2 of sequential removal experiment in Bedrock Pool).

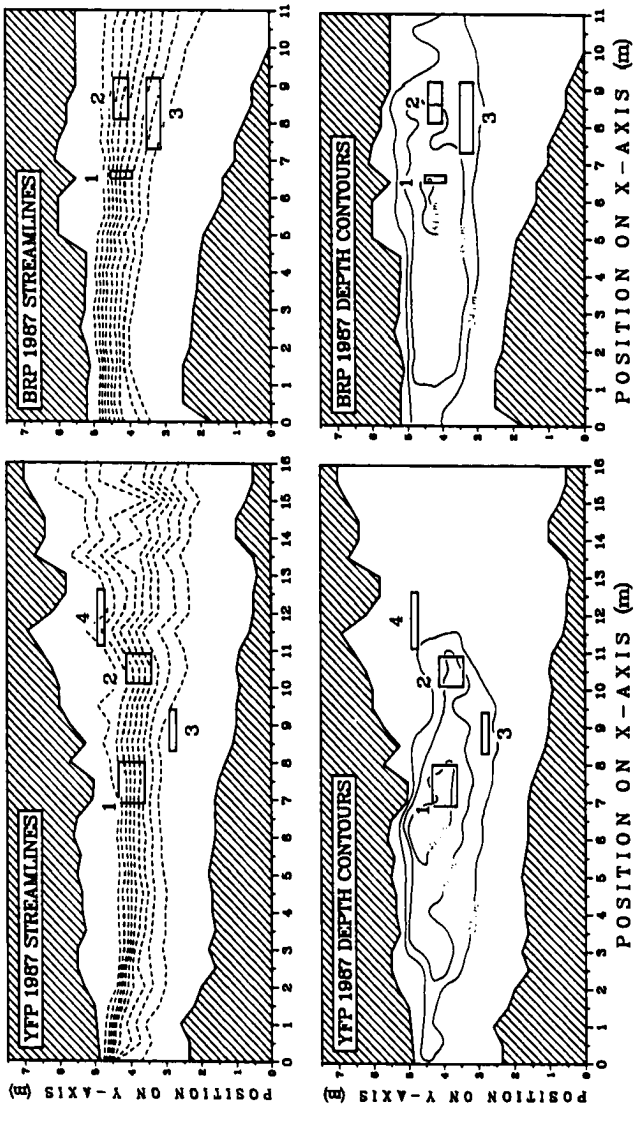


Fig. 3.10. Depth contours and streamlines for Yellow Flower and Bedrock Pools. The numbered boxes show the location and ranking of positions actually used by Arctic grayling in these pools. The depth contour levels were selected to demonstrate important features in the bottom topography.

Discussion

Each fish in the dominance hierarchy should select the position that maximizes its fitness, within the constraints placed on it by dominant fish, and the opportunities provided by the habitat. From this perspective the question - what determines the location and ranking of the feeding positions selected by drift-feeding salmonids in a dominance hierarchy? - has several complementary answers: in this section I examine some of these. I begin with a question about the adaptive value of position choice - do fish locate and rank positions based on the net energy intake rate that these positions provide? Next, I discuss the way in which social restrictions on position choice, and the processes that influence invertebrate drift density, combine to determine the location and ranking of positions. Finally, I discuss the way in which the physical habitat of the pool provides the template for fish distribution by controlling the processes that determine the location and ranking of the most profitable positions.

Adaptive Value of Position Choice

This study supports the hypothesis that Arctic grayling select and rank positions based on potential net energy intake. This conclusion is based on the close fit between the predicted and observed location and ranking of positions (Figs. 3.7 and 3.8). These results support Fausch's (1984) conclusions on the adaptive significance of position choice, but they do not support Jenkins' (1969) and Bachman's (1984) view that there are no variations in feeding opportunity between positions. These results also suggest that trade-offs involving predation risk are

not important in determining the location of feeding positions, as suggested by Newman (1956), Jenkins (1969), and Fausch and White (1981), since it was not necessary to include the effects of predation risk to make fairly accurate predictions of position choice (see Chapter 1 for more discussion).

Role of Individual Processes

A comparison of the predictions of the full model (Fig. 3.7), with the predictions of the four reduced models (Fig. 3.9), shows that all four reduced versions made worse predictions than the full model. This suggests that each of the processes included in the model makes a significant contribution to the model's accuracy.

The predictions of the "no restricted area" model show that, given freedom of choice, subordinates would select positions directly upstream of higher ranking fish. This demonstrates the importance of social behavior in creating distribution patterns where subordinates occupy positions downstream and/or to the sides of the positions occupied by higher ranking fish.

The predictions of the "no prey depletion" model show that the reduction in drift density by a feeding fish makes it unprofitable for subordinates to occupy positions immediately downstream. The effect of this process complements the effect of social restrictions on position choice, because it spaces fish out downstream and/or laterally behind the dominant fish.

Predictions of the "no re-suspension" model show that the replenishment of drift density by re-suspension induces fish to select positions some distance downstream, but directly in line with, the positions occupied by higher ranking

fish. This complements one of the effects of social behavior (spacing fish out downstream) but counteracts another (inducing fish to select positions directly downstream of higher ranking individuals).

Predictions of the "no lateral diffusion" model suggest that the redistribution of prey downstream of a feeding fish has a similar effect to re-suspension, causing fish to select positions some distance downstream of, but in line with, the positions used by dominants.

Physical Habitat as a Template

The bottom topography of the pool and the pattern of current flow determine the volume of water from which the fish can catch prey and the fish's swimming costs (Chapter 1). These two factors also influence lateral diffusion and the re-suspension of invertebrates, processes that determine spatial variation in the density of prey. Because of these influences on the factors that determine NEI these physical characteristics of the pool can be thought of as the template that determines the location and ranking of positions selected by the fish. The importance of the habitat as a template is well illustrated by the relationship between physical characteristics and the location and ranking of positions, shown in Fig. 3.10. Bedrock Pool and the upper 11 m of Yellow Flower Pool are very similar in physical layout and this similarity has produced a corresponding similarity in the location and ranking of predicted and observed positions.

To visualize the way in which the habitat acts as a template for distribution, it is helpful to think about the factors influencing the fish's energy intake at a position in the following way - the number of prey a fish sees increases with water depth,

water velocity, and the density of prey in the water. The proportion of these prey that the fish is able to capture declines with increasing water velocity while its swimming costs increase with water velocity (Chapter 1). The fish must select a position where the combination of these factors maximizes its net energy intake and yet comply with the restrictions on its freedom of choice imposed by higher ranking fish.

For the dominant fish, this position is just downstream of the deepest point, in the center of the current (see Chapter 1 further discussion). For the number 2 fish the small depression about 2 m directly downstream of the dominant fish apparently provides the best compromise between favorable physical characteristics and prey density. These positions are close enough to the center of the current and the deepest part of the pool to provide desirable water depth and velocity characteristics, and yet far enough downstream of the dominant fish's feeding area for re-suspension and lateral diffusion to have substantially replenished the density of drifting invertebrates. For the third and fourth fish, the best compromise is apparently to hold position in scallops in the stream bed at the sides of the pool. Given their distance from the center of the current, these positions provide reasonable depth (because they lie in scallops) and flow (because of the lateral water movement at these positions) and receive water that has skirted either side of higher ranking fish's feeding areas; this means that the prey density at these positions is higher than at physically comparable positions immediately downstream of the second fish.

Future Developments

The model's predictions were encouragingly accurate but it did make several errors. For example, the position predicted for the third fish in Yellow Flower Pool was too near the center of the current while its prediction for the fourth fish was too far downstream. There are several possible reasons for these kinds of errors and they all relate to the fact that the model includes only rough approximations of real processes. Future work should allow more accurate predictions by improving our knowledge of these processes; at the moment the processes included in the model are virtually unstudied in relation to fish distribution.

It would also help if we knew the proximate cues or "rules of thumb" that fish use to locate and rank feeding positions. This too is an unexplored field.

Conclusions

What determines the location and ranking of the feeding positions selected by fish in a dominance hierarchy? I have tried to show that there is more than one answer to this question. In one sense the distribution pattern is the result of each fish seeking the position that maximizes its net energy intake rate, within the constraints placed upon its freedom of choice by higher ranking fish. In another equally valid sense, the pattern is the consequence of the pool's bottom topography, and the pattern of water flow. In this work I have described a foraging model that states explicitly how these two answers are linked together by showing how the physical habitat determines the location and ranking of the most profitable positions.

CHAPTER 4

Why do Arctic grayling get bigger as you go upstream? [1]

Abstract

During the summer Arctic grayling in interior Alaskan streams get bigger as you go upstream. We used a fish removal experiment to test two hypotheses that account for this size-gradient; the experimental results supported the hypothesis that the size-gradient is produced by large fish exclude smaller ones from desirable positions in headwater reaches - rather than the hypothesis that fish-size dependent habitat preferences produce the size-gradient. The predictions of a foraging model supported the hypothesis that Arctic grayling prefer feeding positions in upstream reaches because they are more profitable than positions further downstream; the reason for this gradient in profitability is that the concentration of drifting invertebrates increases as you go upstream.

[1] This chapter is in preparation for submission to the Canadian Journal of Fisheries and Aquatic Sciences as Hughes, N .F., and J. B. Reynolds. Why do Arctic grayling get bigger as you go upstream?

Introduction

In the mountain streams of interior Alaska Arctic grayling *(Thymallus arcticus)* get bigger as you go upstream. Younger fish concentrate in the lower reaches of the river, and the age and length of fish increases steadily with the passage upstream, as far as the second order headwaters (Fig 4.1). This whole-stream size-gradient is a feature of the summer distribution pattern (mid June to late August); it is established soon after spring spawning and breaks down again in the fall, as fish move to overwintering areas.

The increase in size of Arctic grayling with the progression upstream is well documented, but unpublished, in reports by the Alaska Department of Fish and Game (see Armstrong 1986 for review). Information on whole-stream size-gradients of other species of stream salmonids is even harder to find, and this makes it difficult to determine whether the increase in size observed with Arctic grayling is the exception or the rule. There is evidence that some other species of stream salmonids do get bigger as you go upstream: data in McPhee (1966) shows that cutthroat trout *(Oncorhynchus clarki)* and brook trout *(Salvelinus fontinalis)* increased in average size with the progression upstream over about 3.5 km of an Idaho mountain stream, while data in Allan (1975) suggests that brown trout *(Salmo trutta)* and brook trout increased in size with the progression upstream over about 16 km of a Colorado mountain stream. However, whenever the subject of size-gradients is explicitly discussed there is a consensus that fish usually get smaller as you go upstream, salmonids and non-salmonids alike (Brown 1975;

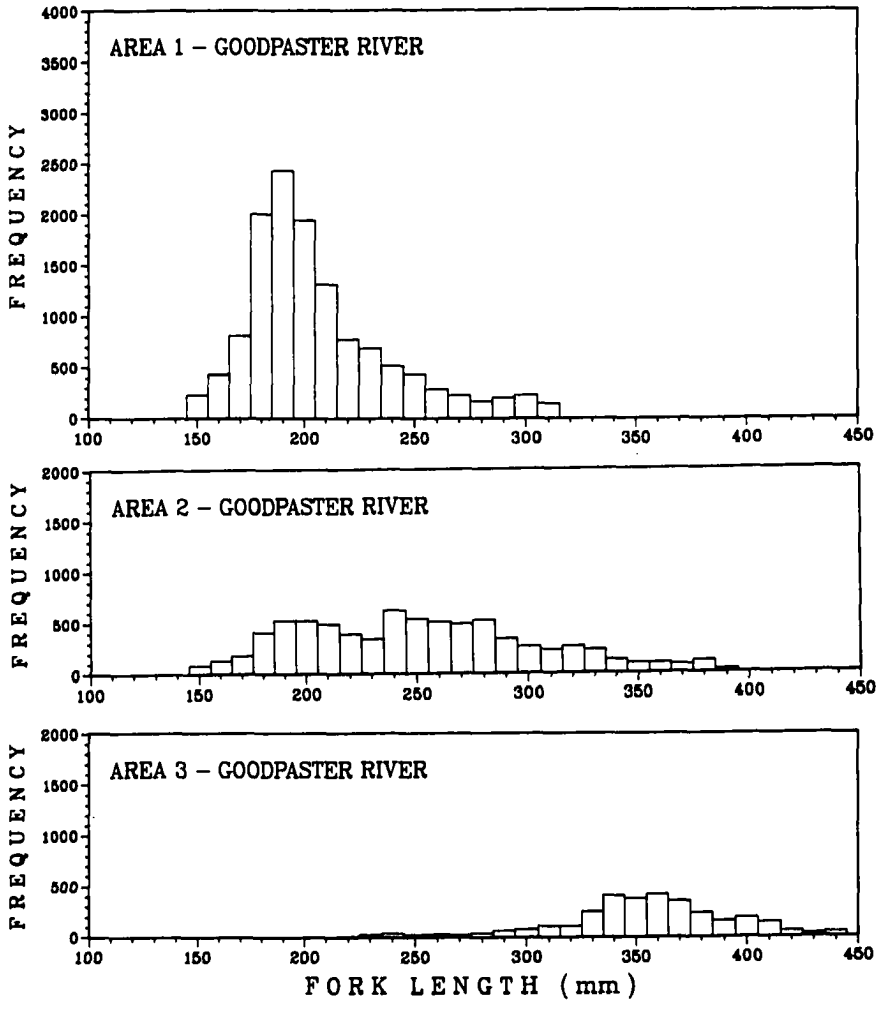


Fig. 4.1. Length-frequency distribution of Arctic grayling in the Goodpaster River, Yukon Drainage, interior Alaska, showing the increase in fish size with the progression upstream. Area 1 includes the lower 53 km of the river, Area 2 the middle 45 km, and Area 3 the upper 87 km (from Tack (1974) with permission).

Patrick 1975; Milner et al. 1978; Smith 1981; Schlosser 1982; Anderson 1985; Ford and Mercer 1986).

Since so little attention has been paid to whole-stream size-gradients it is not surprising that there have only been a few attempts to explain them. Smith (1981) suggested that mortality rates increase, and growth rates decrease, with the progression upstream - and that this favors early maturity and small adult size in the smaller streams. In contrast Anderson (1985) proposed that mortality rates of sculpins *(Cottus bairdi* and *C. cognatus)* decrease with the progression upstream, and that this resulted in higher densities, increased competition for food, slower growth, and smaller adult body size in the smaller streams. Ford and Mercer (1986) suggested that American eels *(Anguilla rostrata)* decrease in size with the progression up tidal marsh creeks because big eels exclude smaller ones from preferred territories in the larger creeks.

Some components of these explanations are complimentary, others contradictory; but one point of consensus among these authors is that whole-stream gradients in foraging opportunity and risk of mortality, are probably the ultimate cause of size-gradients. However, there is no agreement on how foraging opportunity or mortality risk varies along whole streams. Variations in foraging opportunity will depend on the feeding habits of the species in question (Angermeier and Karr 1983). Variations in predation risk will depend on the predator in question; fish predators are usually larger, more numerous, and more effective in the deeper water provided by larger streams (Power 1987; Schlosser 1987), while avian and terrestrial predators may be more effective in small shallow streams (Power 1987; Heggenes and Borgstrøm 1988).

Variation in feeding opportunities and mortality risk may be the ultimate cause of size-gradients - but what are the mechanisms that actually convert these environmental factors into patterns of fish distribution? If fish live out their lives in a short section of a stream, then variations in growth rate, or life history, could account for size-gradients; but when fish are more mobile - then fish-size dependent habitat preferences, or exclusion of small fish of desirable areas by large individuals, should be more important. The brown trout is a fish that spends most of its life in a short stream section (Solomon and Templeton 1976; Bachman 1984; Hesthagen 1988), and decreasing growth rate with the progression upstream can explain why fish get smaller as you go upstream (Frost and Brown 1967): however, fish-size dependent habitat preferences do contribute to the size gradient of brown trout, because mature fish spawn in small streams, and young fish spend a year or two rearing there, before dropping downstream (Solomon and Templeton 1976; Milner et al. 1978; Baglinière et al. 1989). In contrast, Arctic grayling are much more mobile, and size-gradients are mainly the result of older, larger, fish becoming more common as you go upstream, not variation in growth rates: in this case either fish-size dependent habitat preferences, or competition for desirable positions in upstream reaches, is probably the mechanism that produces the size-gradient.

In this paper we present the results of an investigation into why Arctic grayling get bigger as you go upstream. We used a removal experiment to test the hypothesis that the whole-stream size-gradients are produced by competition for desirable feeding positions in upstream reaches (the "sorting between ranked positions" hypothesis); our alternative hypothesis was that fish-size dependent

habitat preferences produced the size-gradient (the "size dependent habitat preference" hypothesis). We used a foraging model to test the hypothesis that Arctic prefer grayling feeding positions in upstream reaches because they allow higher rates of net energy intake than positions further downstream.

Methods

We begin by describing the drainage in which we studied Arctic grayling size-gradients, and the methods we used to determined fish distribution. Next, we explain the experiment and logic that we used to test hypotheses about the processes that produce the size-gradient. Finally, we describe the modeling work we did to test the hypothesis that Arctic grayling prefer positions in upstream reaches because they are more profitable than positions further downstream.

Study Area

Twelvemile Creek is a small stream in interior Alaska (Fig. 4.2), it is a tributary of Birch Creek, which in turn, is a tributary of the Yukon River, and very similar to the headwater reaches of most larger rivers in this part of the State. It flows out of the Steese Mountains, which are actually high rolling hills, the underlying rock is quartzite schist and mica schist. The surrounding vegetation is black spruce, birch, alders, muskeg, and, at upper elevations, alpine tundra. Thick clumps of willows grow on gravel bars but there is no real canopy shading the stream. The stream channel is stony bottomed, with occasional bouldery cascades. The climate is subarctic continental, with long cold winters and short summers,

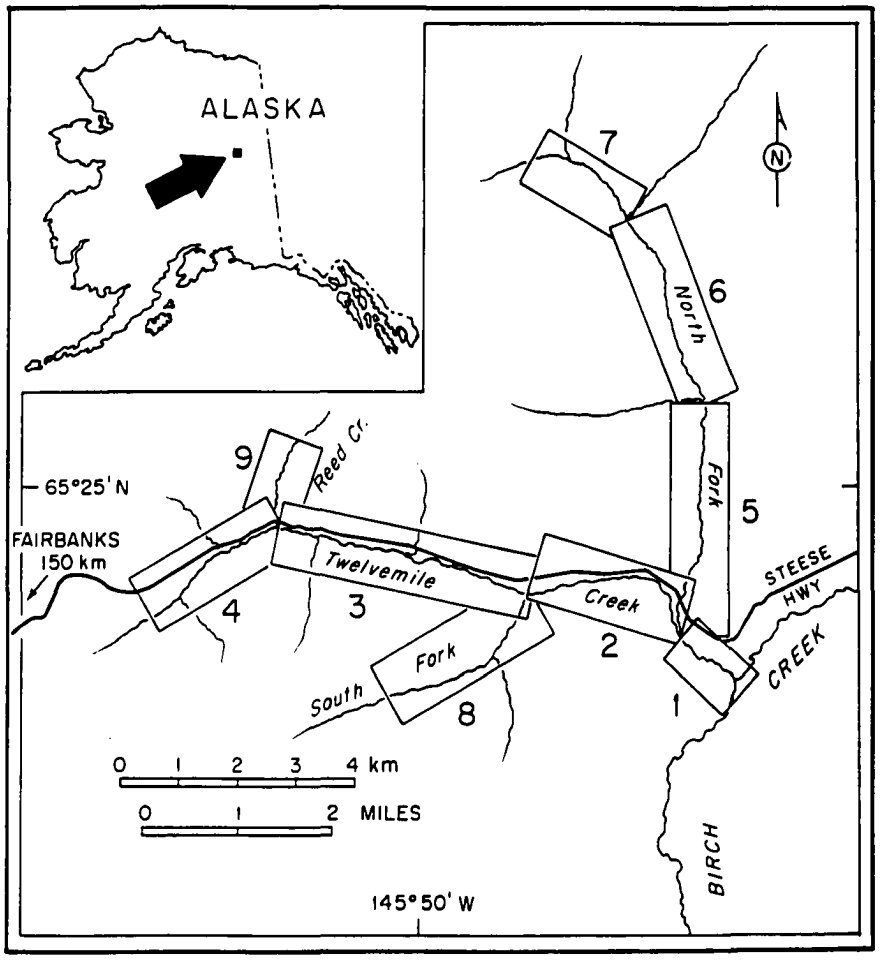


Fig. 4.2. The Twelvemile Creek drainage, showing its division into nine reaches.

the mean annual temperature is -5.5 °C, and the annual precipitation about 288 $mm \cdot y^{-1}$. Twelvemile Creek starts to freeze up in September and is ice covered from October through May. Break up, in late May and early June, is a period of high flow and the water is colored by dissolved organic matter and suspended particulate matter. From mid-June through August the stream generally runs low and clear, except after summer rain storms. Low water discharge during the summer months varies from about 0.03 $m \cdot s^{-1}$ at the upstream limit of grayling distribution, to about 0.6 $m \cdot s^{-1}$ just before its confluence with Birch Creek. It is during the summer months that Arctic grayling distribute themselves throughout Twelvemile Creek, and take advantage of the long summer days to feed. Arctic grayling are abundant and three other species of fish are present; slimy sculpin *(Cottus cognatus)* are common; adult round whitefish *(Prosopium cylindraceum)* and small burbot *(Lota lota)* are present, but neither is abundant.

Twelvemile Creek flows into Birch Creek, which has been heavily polluted with suspended sediments by placer gold mining since about 1975. Arctic grayling avoid the turbidity generated by placer mining (McLeay et al. 1987; Reynolds et al. 1989) and this means that Twelvemile Creek contains a discrete population of Arctic grayling, distributed over a relatively short stream. It was because of this that we chose Twelvemile Creek for an experimental study of Arctic grayling size-gradients.

Fish Distribution

In July and August of 1986 we determined the distribution pattern of Arctic grayling in Twelvemile Creek by electrofishing the entire drainage - from its confluence with Birch Creek to the upstream limit of fish distribution - a total of slightly over 30 km. During the survey we recorded the fork length of each fish that we caught, and the location of its capture. To provide a map with which to describe fish distribution we measured the distance of the downstream end of each pool and riffle from the mouth of Twelvemile Creek.

Before electrofishing each pool and riffle we isolated the section to be fished with blocknets; we then made repeated passes through the section with a Smith Root model VII backpack electrofishing unit,[1] until we had made two consecutive passes without catching any fish. We assessed the efficiency of this method by releasing marked fish into sections before we electrofished them. Our efficiency in pools was very high (98%; 95% CI 88%-100%); our efficiency in riffles was a little lower (85%; 95% CI 69%-94%). Since our attention focuses on the distribution and abundance of fish in pools we treat the electrofishing data as a census.

Fish Removal Experiment

We used a fish removal experiment to determine if the "sorting between ranked positions" hypothesis, or the "size dependent habitat preference" hypothesis, provides the best explanation for Arctic grayling size-gradients. In this section

[1] Reference to trade names or manufacturers does not imply government endorsement of commercial products.

we describe the big fish removal experiment, give the justification for each of the hypotheses, and explain how we used each hypothesis to predict the outcome of the fish removal experiment.

Experimental design

During the course of the 1986 electrofishing survey, and using a fish-weir at the mouth of Twelvemile Creek in September 1986, we removed almost all fish over 260 mm fork length, and 50 fish between 200 and 260 mm fork length (Fig. 4.3); in total we removed 18% of the electrofishing catch (214 fish out of 1209). The purpose of this removal was to produce a population that would be smaller than the 1986 population, and have a different size-structure. By comparing the distribution pattern adopted by this altered population, with the distribution patterns predicted by two hypotheses, we hoped to determine which hypothesis provides the best explanation for Arctic grayling size-gradients.

We followed up the removal experiment in 1988 by electrofishing all 106 pools in reaches 1-4. There were only 286 fish in these pools in 1988, compared to 399 in 1986 (a 28% reduction in numbers), and the length-frequency distributions were markedly different (Fig. 4.4). Experimental fish removal, and natural population processes, obviously combined to produce these changes in population structure - but the objective the experimental fish removal was met.

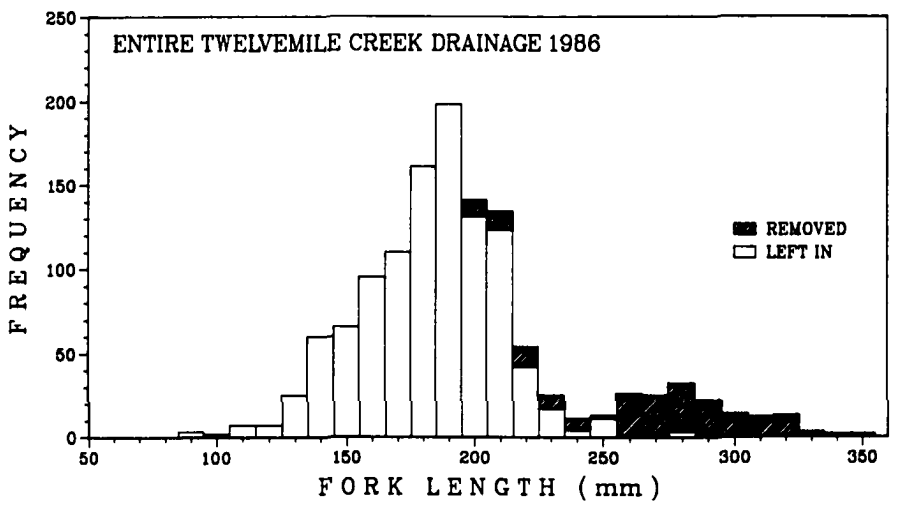


Fig. 4.3. Length-frequency distribution of Arctic grayling in the Twelvemile Creek drainage during the summer of 1986 - showing the size-distribution of fish taken from the stream during the fish removal experiment.

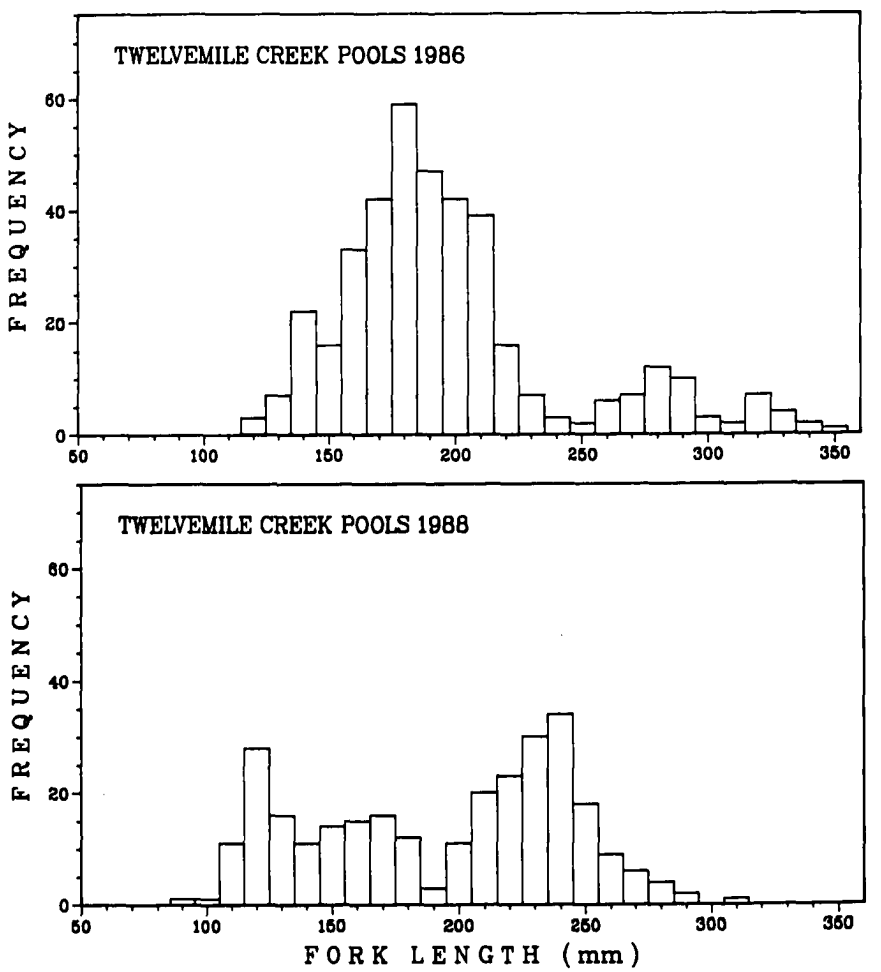


Fig. 4.4. Length-frequency distribution of Arctic grayling inhabiting pools in reaches 1-4 of Twelvemile Creek during 1986 (399 fish) and 1988 (286 fish).

Hypothesis 1: sorting between ranked positions

Within single pools, Arctic grayling rank feeding positions according to desirability, and competition for these positions sorts fish so that the dominance rank of each individual corresponds to the rank desirability of its position (Chapter 2). We hypothesize that the same processes also determine the distribution pattern of Arctic grayling populations over whole-streams. From this perspective the entire stream can be visualized as a series of ranked feeding positions - among which competition has sorted fish, so that the dominant (biggest) fish in the population occupies the most desirable position, and progressively lower ranking (smaller) fish occupy progressively less desirable positions.

If this hypothesis is true then fish distribution in 1986 can be used to estimate the location and ranking of feeding positions; the location and ranking of each position should correspond to the location and rank fork length of each fish. These estimates of location and ranking can then be used as a template, to predict the position of each fish caught during 1988 (such a template, for the pools in reaches 1-4, is shown in Fig. 4.5), the largest fish caught in 1988 is assigned to the same position as the largest fish caught in 1986 - and so on for progressively smaller fish, until all the 1988 fish have been allocated.

Hypothesis 2: size-dependent habitat preference

It is possible that fish-size dependent habitat preferences are responsible for whole-stream size-gradients, rather than the sorting of fish between ranked positions. This could occur if small fish prefer positions in downstream reaches,

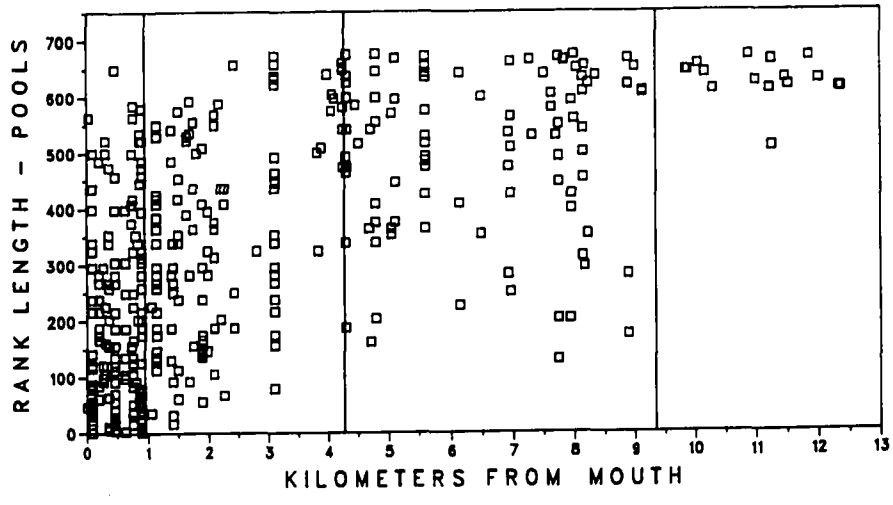


Fig. 4.5. Rank fork length of fish inhabiting pools in reaches 1-4 of Twelvemile Creek during 1986. Ranking is based on fish in both riffles and pools (671 fish in total), 399 fish of these fish inhabited pools. The vertical lines show the reach boundaries.

and progressively larger fish prefer positions progressively further upstream. According to this hypothesis social interaction play no part in producing the distribution pattern.

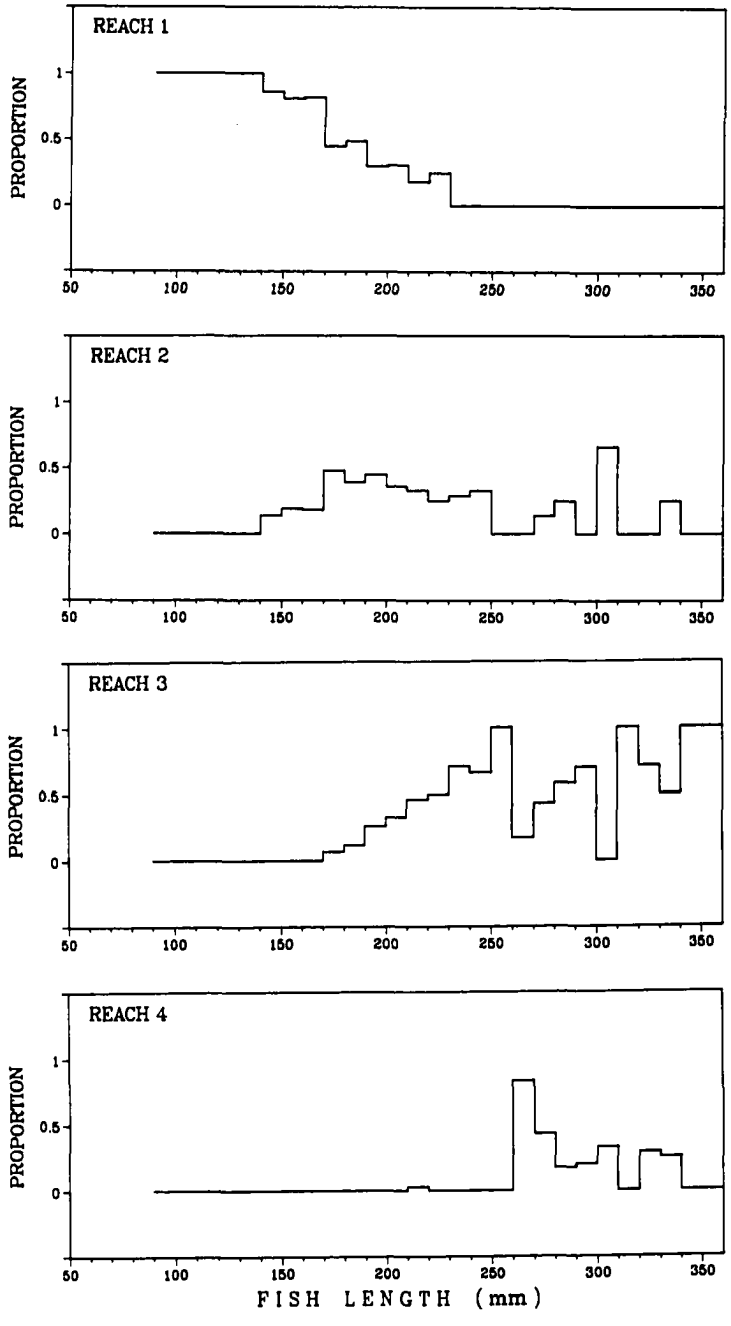
If this hypothesis is true then fish-size dependent preference, for the pools in reaches 1-4, can be estimated from the 1986 distribution pattern - by calculating the proportion of each 1 cm length-class residing in each of the four reaches (Fig. 4.6). To predict the distribution of fish in 1988 we used these proportions to allocate the population of fish actually caught during 1988 among the four reaches.

Whole-Stream Gradients in Feeding Opportunity

Within a single pool Arctic grayling rank and select feeding positions on the basis of net energy intake rate (Chapter 1; Chapter 3). We hypothesize that this is also the basis for the ranking and selection of feeding positions over the length of the entire stream, and that Arctic grayling prefer positions in upstream reaches because these are more profitable than positions further downstream. One reason for such a gradient in profitability is the inverse relationship between mean summer discharge and invertebrate drift concentration in interior Alaskan streams (LaPerriere 1981; 1983; equation given in Table 1.3).

To test this hypothesis we used Hughes and Dill's (Chapter 1) model to predict the maximum net energy intake rate possible in each of the 106 pools in reaches 1-4. According to the hypothesis this should increase with the progression upstream. We made these predictions using a single depth and velocity profile (25 cm measurement interval), that we took across the deepest part of each pool during 1986; this should provide a reasonable estimate of the maximum net energy intake

Fig. 4.6. Allocation of each 1 cm length class of Arctic grayling between reaches 1-4 of Twelvemile Creek, 1986, pool fish only. Note that there were no fish smaller than 12 cm caught in 1986 and the allocation of fish <12 cm fork length was estimated at 1.0 for reach 1 and 0.0 for reaches 2, 3, and 4, based on the fact that 100% of fish in the 12 and 13 cm length groups inhabited reach 1 during 1986. This extrapolation was necessary because 13 fish <12 cm were caught during 1988.



rate possible in the pool, because the most profitable position is usually close to the deepest point (Chapter 1). We accounted for the influence of stream size on drift concentration by estimating the mean summer discharge (SF) through each pool from the regression: $SF = 0.573 - 0.00530 \cdot POOLNUMBER$; R^2=87; where $POOLNUMBER$ increases from 1 to 106 with the progression up reaches 1-4. We then calculated drift concentration from SF using the appropriate equation from Table 1.3.

To see if a gradient in feeding opportunities would exist if drift concentration did not increase with the progression upstream we also predicted the maximum net energy intake in each pool using using a single drift concentration, which we calculated using the mean discharge for all 106 pools (0.3 $m^3 \cdot s^{-1}$).

In all these simulations we used a 20 cm fish; using a smaller (15 cm) or larger (35 cm) fish did not change the results significantly.

Results

Fish Distribution in 1986

The distribution of Arctic grayling throughout the Twelvemile Creek drainage is shown in Fig. 4.7 and Table 4.1; as in larger rivers there is an increase in fish length as you go upstream, although the size-gradient is less pronounced than over the length of the Goodpaster River (Fig. 4.1).

Fig. 4.7. Length-frequency distribution of Arctic grayling in reaches 1-9 of Twelvemile Creek during 1986.

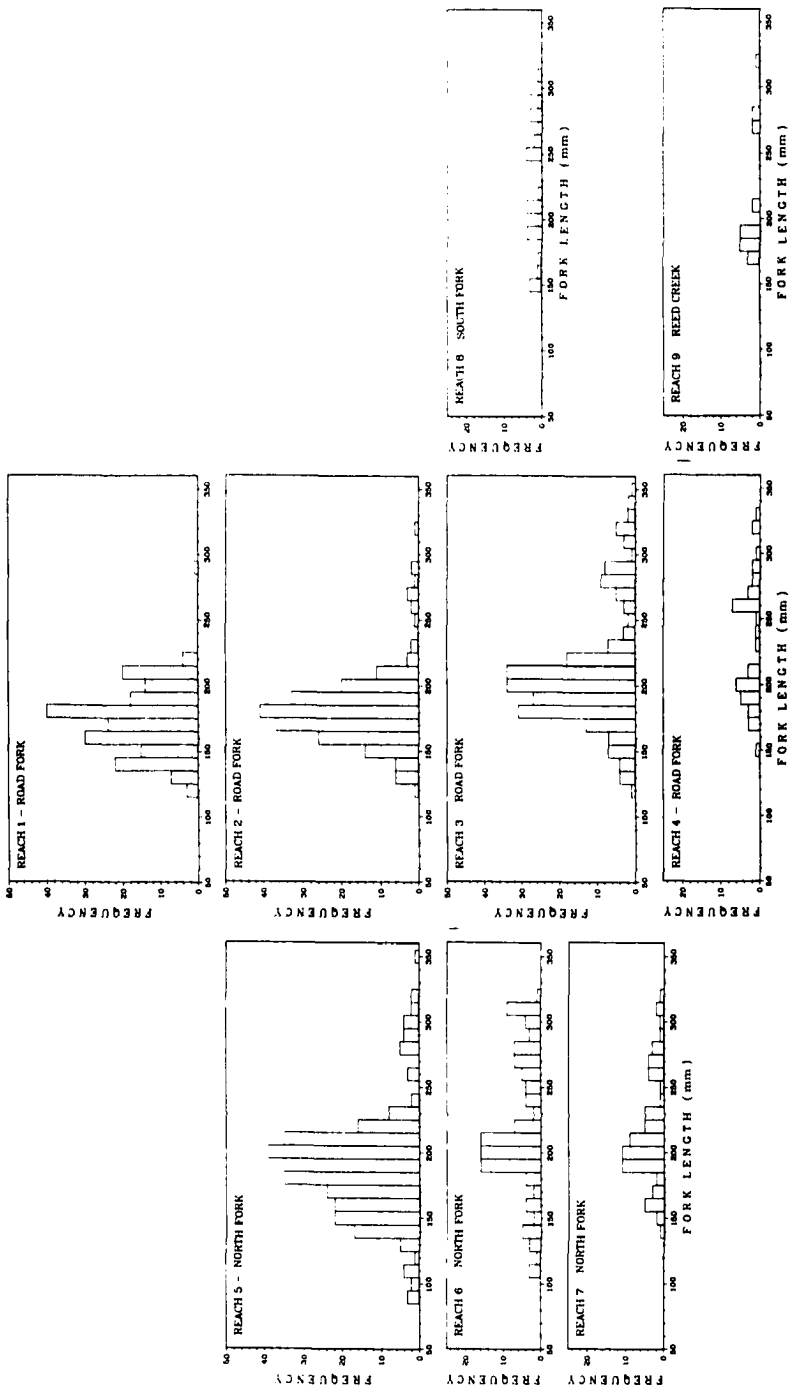


Table 4.1. Abundance and mean fork length of Arctic grayling in reaches 1-9 of Twelvemile Creek. Showing length of reach, number of fish caught in each reach, number of fish per kilometer, and mean fork length.

Reach number	Reach length (km)	Number of fish	Fish abundance No·km^{-1}	Mean fork length (cm)
Road Fork				
1	0.952	188	197	18.8
2	3.314	210	63	19.7
3	5.074	231	46	21.5
4	3.029	42	14	23.7
North Fork				
5	4.465	291	65	19.4
6	3.185	125	39	22.4
8	3.189	72	23	22.1
South Fork				
8	5.032	30	6	23.6
Reed Creek				
9	1.400	20	14	21.5

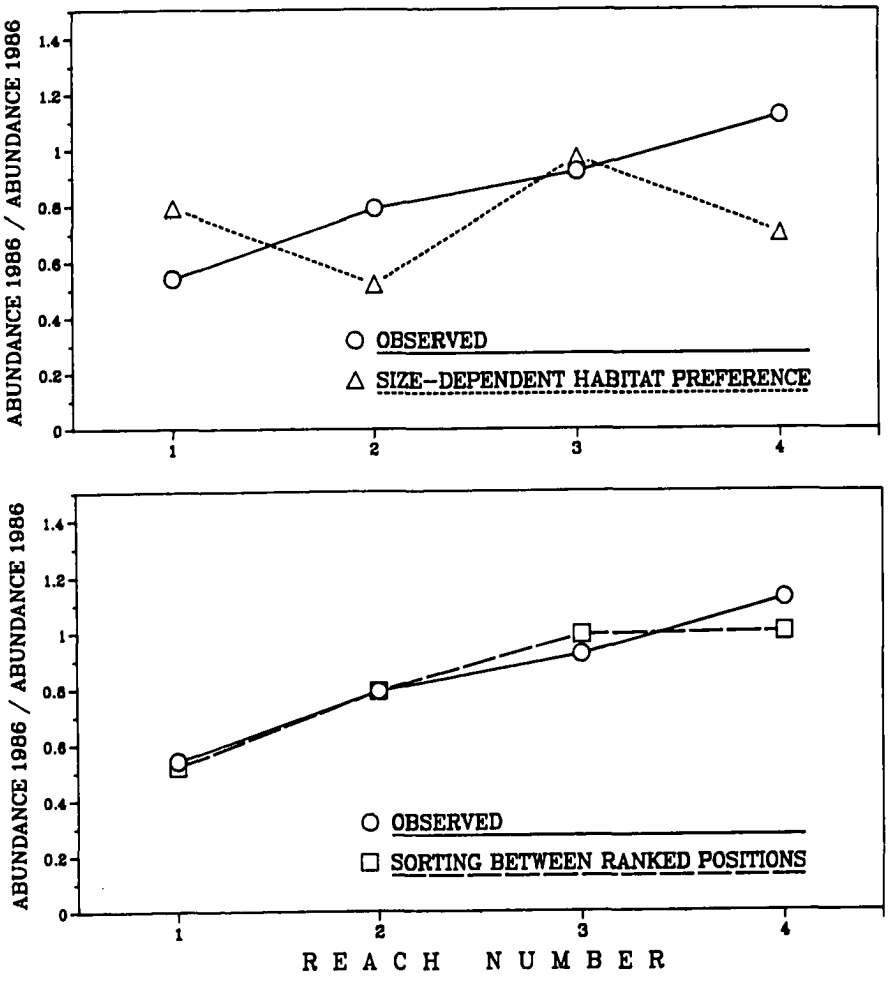


Fig. 4.8. Comparison of predicted and observed abundance of fish inhabiting pools in reaches 1-4 of Twelvemile Creek during 1988. Top: predictions of the "size-dependent habitat preference" hypothesis are compared with observed abundances. Bottom: predictions of the "sorting between ranked positions" hypothesis are compared with observed abundances. Abundance in 1988 is expressed as a proportion of the abundance in 1986.

Big Fish Removal Experiment

The predictions of fish abundance that the two hypotheses made for reaches 1-4 are compared to the abundances actually observed in Fig. 4.8. The predictions of the "sorting between ranked positions" hypothesis fit the observed values very well, and they are considerably better than the predictions of the "size dependent habitat preference" hypothesis. In fact the "sorting between ranked positions" hypothesis leaves only 2% as much unexplained variation as the "size dependent habitat preference" hypothesis.

The length-frequency distributions predicted by the two hypotheses are compared to the observed length-frequency distributions in Fig. 4.9. Again the predictions of the "sorting between ranked positions" hypothesis are better than the predictions of the "size dependent habitat preference" hypothesis. The "sorting between ranked positions" hypothesis leaves only 36% as much unexplained variation as the "size dependent habitat preference" hypothesis. The distributions predicted by the "sorting between ranked positions" hypothesis mirror the observed distributions - both in the size range of fish, and in the abundance of each length class. In contrast, the "size dependent habitat preference" hypothesis usually predicts a truncated size distribution, compared to the observed size range, and its predictions of abundance for each length class are considerably worse.

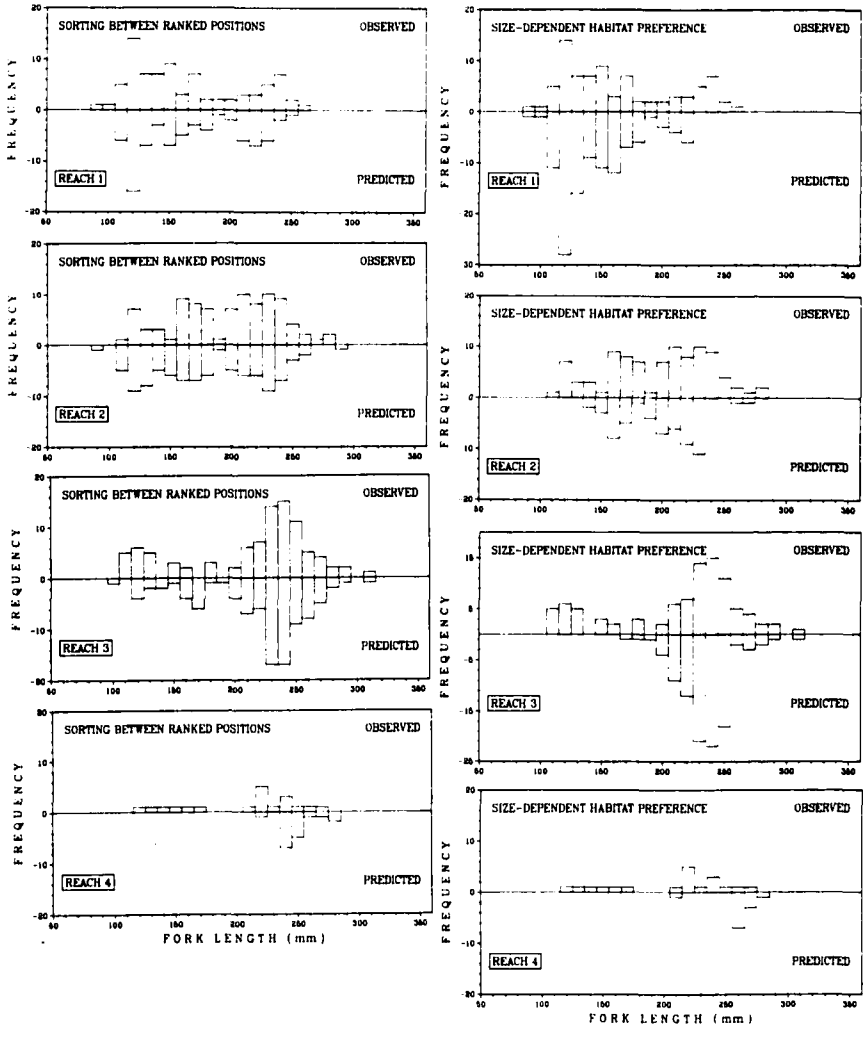
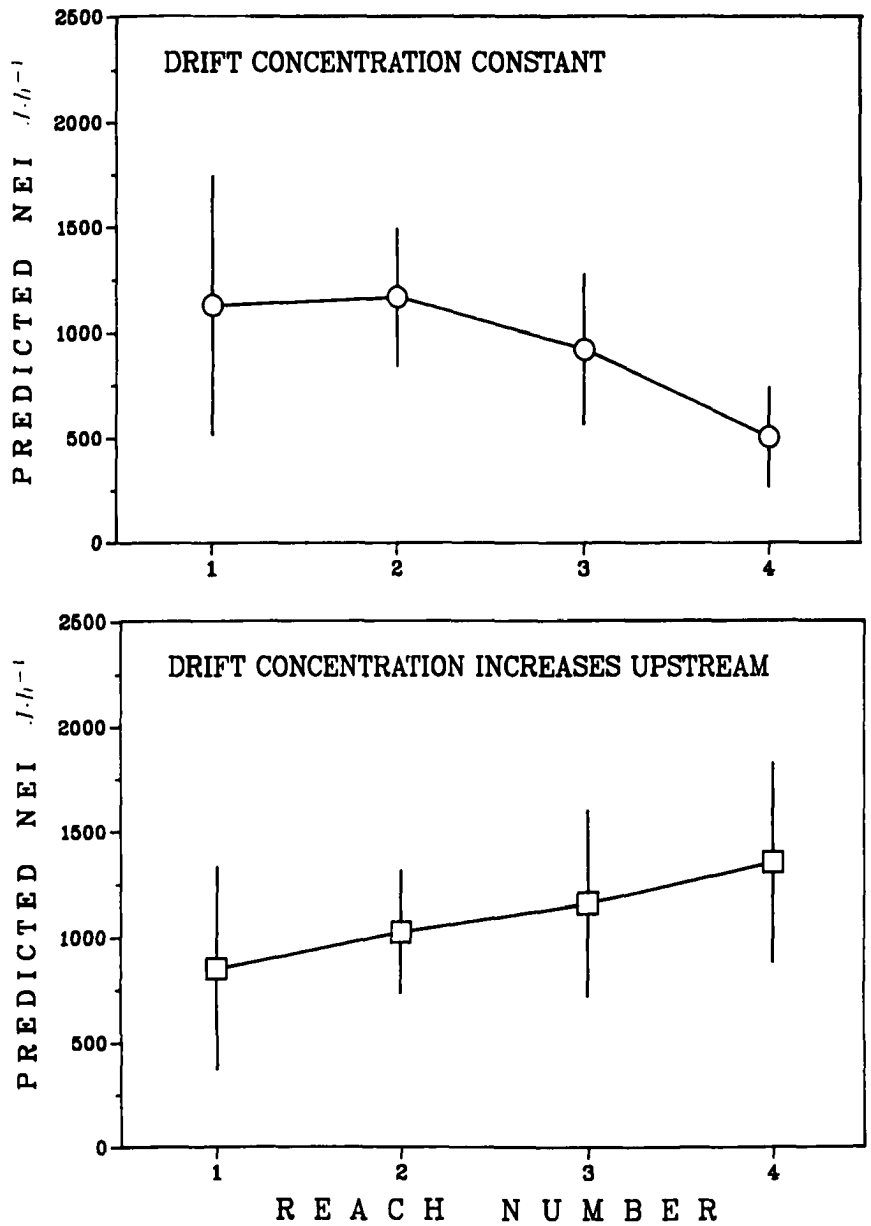


Fig. 4.9. Comparison between predicted and observed length-frequency distributions of fish inhabiting pools in reaches 1-4 of Twelvemile Creek during 1988. Left panels: predictions of the "sorting between ranked positions" hypothesis are compared to the observed distributions. Right panels: predictions of the "size-dependent habitat preference" hypothesis are compared with the observed distributions.

Fig. 4.10. Relationship between predicted maximum net energy intake rate in the pool, and reach number, reaches 1-4 of Twelvemile Creek. Based on reach means for the 106 pools in reaches 1-4. Top: predictions under the assumption of constant invertebrate drift concentration. Bottom: predictions under the assumption that drift concentration increases upstream. Bars show ±1 SD.



Whole-stream Gradients in Feeding Opportunity

The predictions of the foraging model supported the hypothesis that feeding positions become more profitable as you go upstream. However, if drift concentration is held constant then the predicted net energy intake actually decreases as you go upstream (Fig. 4.10). Regression analysis of predicted net energy intake (NEI) on distance upstream, using data from the 106 pools in reaches 1-4 shows that, although these gradients in predicted profitability are highly significant, there is a lot of variation that is not accounted for. When drift concentration increases upstream the regression was $NEI = 891 + 39.9 \cdot KMFROMMOUTH$; $p<0.001$; $r^2=0.12$; when drift concentration is held constant the regression was $NEI = 1281 - 61.8 \cdot KMFROMMOUTH$; $p<0.001$; $R^2=0.27$.

Discussion

This study supports the hypothesis that whole-stream size-gradients of Arctic grayling are the result of large fish excluding smaller ones from profitable feeding positions in the upper reaches of streams.

The hypothesis that large fish exclude smaller ones from desirable positions in the headwater reaches was supported by the fish removal experiment. The fish distribution observed in 1988 was closely matched by the predictions of the "sorting between ranked positions" hypothesis, but not by the predictions of the "size-dependent habitat selection" hypothesis.

The hypothesis that fish prefer positions in upstream reaches because they are more profitable was supported by the foraging model, which predicted an increase in the profitability of feeding positions with the progression upstream. However, almost every ecological factor varies with stream size (Vannote et al. 1980; Naiman et al. 1987), and there are plenty of alternative explanations for the Arctic grayling's preference for upstream reaches.

These results show that the same processes which determine the distribution patterns adopted by Arctic grayling in pools (Chapters 1, 2, and 3), also determine the distribution of populations of fish over whole streams. At both spatial scales it appears that fish rank positions on the basis of profitability, and that competition sorts fish so that the largest (dominant) fish occupies the most desirable position, and progressively smaller (lower ranking) individuals occupy progressively less desirable positions.

SUMMARY AND CONCLUSIONS

1. A close match between the positions predicted by a foraging model, and those selected by solitary Arctic grayling, supported the hypothesis that fish choose positions which maximize their net energy intake rate.

2. Water velocity and water depth are the two most important environmental variables determining the profitability of positions to solitary Arctic grayling. To maximize their net energy intake rate fish must make a trade-off between the rate at which they can detect prey, and the proportion of these they can capture. The number of prey a fish sees increases with water depth and velocity, while the proportion of detected prey it is able to capture declines with water velocity.

3. At mean summer concentrations of invertebrate drift, trade-offs involving swimming costs are not very important in determining the location of feeding positions. However, at low drift concentrations swimming costs are important.

4. Field experiments demonstrated that, when groups of Arctic grayling share a pool, they rank feeding positions according to desirability, and competition sorts fish so that the dominance rank of each individual (which is determined by its size) matches the rank desirability of its position.

5. The fit between the predictions of the foraging model, and the positions selected by Arctic grayling in dominance hierarchies, supports the hypothesis that fish locate and rank positions based on potential net energy intake rate.

6. To maximize their net energy intake, fish in dominance hierarchies must select a position which provides the best combination of water depth, water velocity, and drift concentration, and still complies with the restrictions imposed by higher ranking fish.

7. Because of its influence on the factors that determine a fish's net energy intake rate, the physical habitat is the template that determines the location and ranking of positions selected by fish in a dominance hierarchy.

8. Experimental and modeling work supported the hypothesis that whole-stream size-gradients of Arctic grayling are the result of large fish excluding smaller ones from profitable feeding positions in the upper reaches of streams.

9. Taken together the results of this study show that competition for profitable positions can explain the distribution patterns adopted by solitary Arctic grayling in pools, groups of Arctic grayling in pools, and populations Arctic grayling over entire streams.

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